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## A TEN-YEAR ECOLOGICAL STUDY OF ADJOINING GRAZED AND UNGRAZED WOODLANDS IN NORTHEASTERN OHIO

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# A TEN-YEAR ECOLOGICAL STUDY OF ADJOINING GRAZED AND UNGRAZED WOODLANDS IN NORTHEASTERN OHIO

## INTRODUCTION

The most effective and profitable soil and water conservation practice that farmers can apply to woodlands is the elimination of grazing. Studies conducted by Auten (1941) show, for example, that woodland soils protected from grazing are capable of absorbing rainfall "50 times as fast as comparable field soils." The average loss of water by surface runoff from a protected woodland at the Soil Conservation Experiment Station, Zanesville, Ohio, for a 6-year period was only 3.4 percent of the total rainfall. During the same period, the runoff loss on pasture was 15.2 percent and on cropland, 23.3 percent. Soil losses for the same period were 0.09 ton per acre from woodland, 0.8 ton per acre from pasture, and 133.6 tons per acre from cropland (Borst & Woodburn 1941).

These facts spur conservationists to assist and encourage protection of woodlands from grazing. They are not, however, the kinds of facts to convince farmers that it pays them to fence their woodlands for this purpose. To this end, tangible economic and aesthetic benefits must be demonstrated before livestock will be excluded from the millions of acres of woodland now being depleted by grazing. In an effort to obtain such economic data and to determine the biologic effects of grazing, a study was conducted in a pastured and an adjacent ungrazed sugar maple woodland in Burton Township, Geauga County, Ohio, during the 10-year period between 1932 and 1942.

This study was conducted while the writer was employed by the United States Soil Conservation Service. Many of his associates in this organization have offered helpful suggestions and otherwise assisted in the conduct of the study. Particular thanks are due Dr. R. W. Gerdel for help on the soil studies and to Dr. Warren W. Chase for editing the manuscript and supervising its preparation. Mr. Edward S. Thomas of the Ohio State Museum assisted in obtaining field records during 1942 and Mr. R. M. Kriebel identified the grasses and sedges collected. Dr. E. N. Transeau kindly reviewed the manuscript and offered many helpful suggestions. The study could not have been made without the full cooperation of the woodland owners, F. E. Kibler and Frank Urbanowicz. Mr. Kibler, owner of the ungrazed tract, assisted in laying out plots and in obtaining yearly records of maple syrup production.

## DESCRIPTION AND HISTORY OF AREAS

The areas studied have provided an unusually good opportunity to compare both plant and animal abundance under grazed and ungrazed conditions in

woodlands otherwise very similar. They are contiguous tracts which are separated only by a three-strand barbed wire fence (Figures 1 and 2). One



FIG. 1. Adjacent grazed and ungrazed sugar-maple woodland. Burton Township, Geauga County, Ohio. 1941. The area to the left has not been grazed since the fall of 1931.

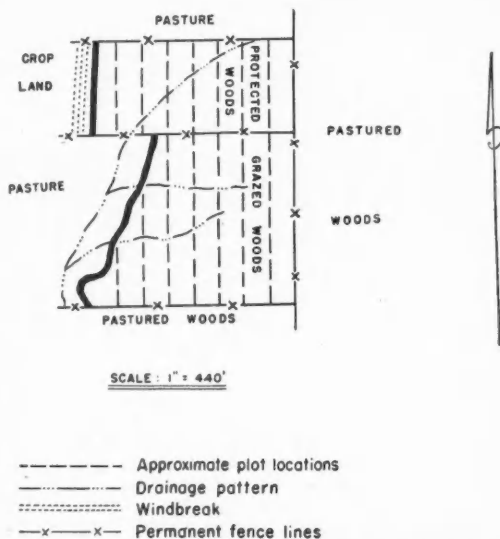


FIG. 2. Orientation of protected and grazed woodlands.

tract comprises 7.9 acres and the other 12.4 acres. Both areas have been managed as maple syrup camps for approximately 50 years. The smaller tract was purchased by its present owner in 1911. The larger area has passed through several ownerships during this time. Both areas were grazed lightly by cattle and horses prior to 1911.

## LAND USE, SOIL AND CLIMATE

The 7.9-acre area was severely grazed from 1911 until the spring of 1932 when a fence was built to exclude livestock. The intensity of grazing varied somewhat from year to year during this period but averaged one animal unit for each acre of pasture and two animal units for each acre of woodland. This area has been continuously protected from grazing since March 1932 and is referred to in this study as the "ungrazed woodland." Less intensive grazing occurred in the 12.4-acre area, referred to as the "grazed" woodland, and, during several seasons between 1911 and 1932 no grazing took place. Between 1932 and 1942, grazing intensity averaged one animal unit per acre of pasture and three-fourths of an animal unit to each acre of woodland.

The size, shape, relative position, adjacent land use and drainage pattern of the two areas are shown in Figure 2. Topography in both tracts is similar, ranging from nearly level in the eastern to gently rolling in the western part. The soils are composed of loam and silt loam of the Canfield and Ravenna soil series. These are upland glacial soils of the late Wisconsin drift. They differ somewhat in the character of the subsoil, degree of acidity, and natural drainage (Mooney et al. 1916, Conrey 1937). The subsoil of the Canfield series is slightly heavier than the surface soil; is pale yellowish-brown, gray mottled below 16 to 24 inches; is acid, and has fair to good natural drainage. The Ravenna series subsoil is slightly heavier than the surface soil. It is only about 8 inches below the surface and is mottled yellowish-brown and gray; natural drainage is poor, and the surface soil is very acid.

The two series are so intermingled in the areas that it is difficult to segregate them. Approximately 60 percent of the ungrazed area is composed of soils of the Ravenna series, 35 percent of the Canfield series, and 5 percent of sandy knolls. In the grazed area the Canfield series comprises approximately 65 percent of the area; the Ravenna series, 30 percent, and sandy knolls 5 percent. The pastured area thus has somewhat better natural drainage and soil porosity than the ungrazed area.

The climate is very favorable for the development of beech-maple forests and for the manufacture of maple syrup (Hill 1904). The winters are long and cold and annual snowfall averages in excess of 60 inches. The short average growing season of 134 days is marked by moderate temperatures and good distribution of rainfall. Average annual temperature is 47.2° F.; maximum temperature, 95° F.; and the minimum officially recorded is 30° F. below zero. The mean annual precipitation is 39 inches.

MANAGEMENT PRACTICES AND CONDITION  
OF THE WOODLANDS

The original composition of both tracts of woodland was probably the beech-maple type with chestnut on the sandy knolls. Selective cutting during

the last 125 years to obtain lumber for construction of buildings, posts for fencing, and wood for fuel has removed most of the white ash, tulip poplar, black cherry, red and white oaks and cucumber magnolia, which were also present in the original forest. This statement is based on material in buildings on the two farms and identification of the remaining stumps in the woodlands.

For the past 50 or more years, both areas have been managed for the production of maple syrup. Practically all of the beech has been cut during this time to provide fuel to boil down maple sap into syrup. Ninety-one percent of the present stand is made up of sugar maple. The remaining 9 percent includes small numbers of red maple, white oak, red oak, tulip poplar, black cherry, beech, cucumber magnolia, white elm, bitternut and shagbark hickories, basswood, tupelo, butternut, and hop-hornbeam.

Tree diameters, at breast height, range from 2 to 36 inches, with the mean being between 10 and 12 inches. Ninety-seven percent of the stand is under 19 inches in diameter. Based on counts of annual rings, the average age of the stand is 65 years. The trees average 72 feet in height and have a crown depth of 38 feet. Due to less severe cutting operations, the ungrazed area had, at the beginning of the study, 107 trees to the acre with an average basal area of 71 square feet per acre as compared with 85 trees with 66 square feet basal area per acre in the grazed area. Basal area was determined by measuring the diameter of all trees in both woods at breast height, approximately 4.5 feet.

At the time the ungrazed woods was fenced to exclude livestock in March, 1932, both woods had reached the transitional stage of forest degeneration (Day 1932, Den Uyl 1938). Seedlings of tree species in both areas were practically absent and only a few stunted colonies of herbaceous plants remained. These included such grazing tolerant species as May apple, partridge berry, grape fern, sedges and several pasture grasses and weeds. Leaf litter was scant or absent in the western part of both areas and had accumulated in the eastern part and in depressions. The roots of many trees were exposed by trampling of livestock, and an abundance of large-sized sandstone fragments at the surface in some places indicated soil loss from water erosion. Grazing injury was much more pronounced in the protected than in the grazed woodland.

During April and May of 1932, 1,500 one-year-old nursery grown white ash seedlings and a total of 500 three-year-old Scotch pine and Austrian pine were set out in openings and along the south and east border of the ungrazed woodland. A 2-row planting of 8-year-old Scotch pine was made also along the west margin of this woods in 1937. Nearly half of this planting failed. In 1938 a 4-row planting of 5-year transplant nursery grown blue spruce was made as a Christmas tree and windbreak planting adjacent to the original Scotch pine and Austrian pine border.

### TIME AND METHOD OF OBSERVATION

Following exclusion of livestock from the 7.9-acre area in 1932, general observations were made to note what effect removal of livestock had on the natural increase of forest trees, of herbaceous plants, of forest wildlife, and of maple syrup production. Observations were made each year on Memorial Day, Fourth of July, and Labor Day and during Christmas week. Beginning with Christmas week of 1937, more detailed observations were made, and permanent sample plots were established in both areas. Changes in vegetation were recorded annually in these plots. As the study progressed, it appeared desirable to investigate additional components of the woodland biota, including invertebrate and small mammal populations. The physical properties of the soil were also studied. A summary of these observations and studies and the data obtained is given below.

### DEVELOPMENT OF YOUNG TREES FROM SEEDLINGS

Protection from grazing did not immediately result in the appearance of seedlings. During 1932 and 1933, no notable difference in seedling development was evident in the two areas. An unusually good seed crop in 1933 was followed the next year by the appearance of thousands of young seedlings, principally sugar maple, in the eastern one-third of the ungrazed area. These seedlings attained an average height of 5 inches and persisted throughout the summer. In the grazed area seedlings also appeared in abundance, but they were practically all destroyed by midsummer. Each succeeding year seedling trees became more abundant and vigorous in the ungrazed area. Development continued most rapidly in the eastern part but by 1938 there was a rather uniform mantle of seedlings covering the entire forest floor. At this time there was an average of 39,800 seedlings per acre (Figure 3) with an average height of 16 inches. In the exposed western part, seedlings ranged from a few inches to a foot



FIG. 3. Close up photograph of reproduction in ungrazed woodland. 1941.

in height, while at the opposite end they varied between 1 and 10 feet. During the same years the grazed woodland went through a seasonal cycle of early seedling development and their removal later by midsummer grazing (Figure 4).



FIG. 4. Close up photograph of forest floor in grazed woodland. August 1942.

In May, 1938, 25 milacre reproduction plots were established in the ungrazed area, and 40 similar plots were set up in the grazed tract. Plot lines were established two chains apart and the plots one chain apart on these lines to avoid bias in their selection. Approximate location of the plots is shown in Figure 1. Records of the number, kind, and vigor of all woody plants found in these plots were obtained during the last week of May in the years 1938 to 1942, inclusive. A summary of the data is shown in Figures 5 and 6. Records were also kept of other species and of individual dominant trees that did not appear in the plots.

As can readily be ascertained from Figures 5 and

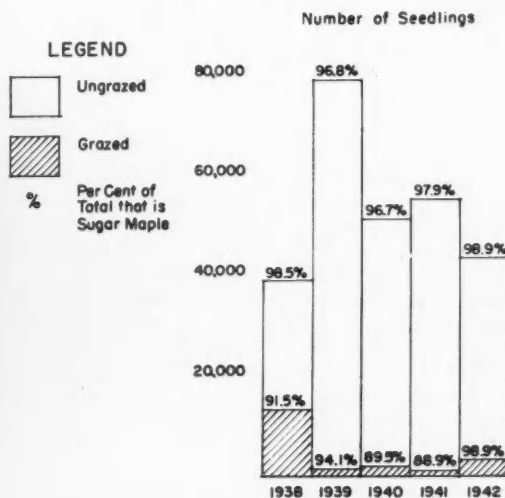


FIG. 5. Natural reproduction. Number of seedlings per acre.

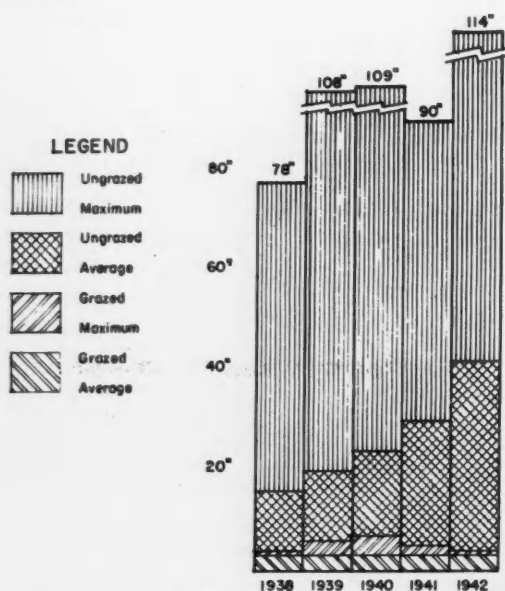


FIG. 6. Natural reproduction. Height of seedlings.

6 sugar maple is the dominant species reproducing in both tracts. Eighteen other species are present, including cucumber magnolia, sassafras, basswood, apple, common junberry, slippery elm, blue beech, shagbark hickory, and tupelo which did not appear in any of the plots.

Tulip poplar and white ash are the only species reproducing which are growing as rapidly as sugar maple. In the eastern part of the woods some of the young trees of this species have outgrown the maples. A few of them already tower 12 feet above the maple clumps. One outstanding tree has attained a height of 23 feet and a diameter of 2½ inches within 8 growing seasons. These individual trees, of which there are now 6 over 2 inches in diameter, usually appear singly in openings where young maples are abundant. They rapidly overtake the maples in both diameter and height growth.

The approximately 50 larger white ash are the survivors of 1,500 one-year-old thrifty seedlings planted in openings in the spring of 1932. They are barely ahead of the maples in height and diameter growth. Most of the planted trees have been overtopped by the thousands of young maples which came up around them. Five hundred Scotch and Austrian pines planted at the same time have been completely shaded out by the abundant hardwood seedlings.

Growth of the remaining species is decidedly slower except for several slippery elms which came up around a tree felled by lightning in 1935 in the western part. These trees have been favored by the fact that until recently growth and establishment of sugar maples in this end of the area was slower than in the interior and eastern parts. The wind-break planted along the western boundary in 1938,

has apparently resulted in increased seedling growth in this part of the woodland. Over the tract as a whole, however, there is a decline in the number of seedlings because of overcrowding.

No marked change in the appearance of the forest floor has taken place in the grazed area since observations were begun in 1932. The number of seedlings per acre has varied each year according to the abundance of the seed crop and the intensity of grazing preceding the time of observation. By mid-summer or early fall of each year only occasional seedlings remain. Invariably these are close to the trunks of trees or beside rocks where they are not so readily reached by livestock (Figures 4 and 7). The



FIG. 7. Tree seed production in the grazed woodland, as illustrated by the abundant wild black cherry fruits shown in this picture, is adequate for natural restocking. By early fall the seedlings produced are usually eaten by cattle except for a few which escape at the base of trees or large stones. August 1942.

seedlings of only five species (sugar maple, red maple, black cherry, red oak and white oak) were found growing in this tract. During the 11 years this area has been under observation, not a single seedling has attained a height of 1 foot and only a few seedlings have lived more than one season.

#### DEVELOPMENT OF HERBACEOUS AND SHRUB SPECIES

The development of herbaceous and shrub species in the ungrazed woodland lagged behind that of tree



reproduction for several years. Only those species which persisted through the grazing period made immediate recovery. The common woodland plants, such as upland ladyfern, spinulose shieldfern, boulder fern, hairy disporum, perfoliate bellwort, rue anemone, and Dutchman's breeches were not evident until 1937 and 1938. Since then the flora of the area has increased greatly both in number of species and abundance of plants. There now are frequent colonies of such plants as large flowered trillium, Jack-in-the-pulpit, wild leek, round-lobe hepatica, Dutchman's breeches, squirrel corn, wild crane's bill, and even two small colonies of ginseng (Figure 8).



FIG. 8. A portion of a colony of ginseng which has developed in the ungrazed woodland since livestock were excluded. August 1942.

The sources of these plants are uncertain. Probably many of them persisted as suppressed specimens that escaped early attention. The presence of some of them in the grazed woods, which were found after an intensive search in 1942, strongly supports this possibility. The seeds of others have probably been brought in by birds and small mammals. This is believed to be particularly true of the shrubby species, such as sassafras, spicebush, paw paw, Virginia rose, hawthorns, and elderberry.

In Table 1 a list of all the vascular plants recorded for both tracts is presented. Some species

TABLE 1. Relative abundance of plants in ungrazed and grazed woodland.

Species <sup>1</sup>		Presence and Abundance <sup>2</sup>	
		Ungrazed	Grazed
<i>Acer rubrum</i> L.	Red maple	Occasional	Occasional
<i>Acer saccharum</i> Marsh.	Sugar maple	Common	Common
<i>Allium tricoccum</i> Ait.	Wild leek	Occasional	Absent
<i>Alsine media</i> L.	Common chickweed	Occasional	Common (In openings)
<i>Amelanchier canadensis</i> (L.) Mod.	Common junberry	Occasional	Absent
<i>Arisaema triphyllum</i> (L.) Torr.	Jack-in-the-pulpit	Common	Occasional (Stunted)
<i>Asimina triloba</i> (L.) Dunal.	Papaw	Occasional	Absent
<i>Aster paniculatus</i> Lam.	Panicle aster	Occasional	Absent
<i>Athyrium angustum</i> (Willd.) Presl.	Upland ladyfern	Occasional	Rare
<i>Botrychium dissectum</i> Spreng.	Cutleaf grapefern	Occasional	(Stunted) Occasional
<i>Botrychium virginianum</i> (L.) Sw.	Virginia grapefern	Occasional	Occasional
<i>Benzoin aestivale</i> (L.) Nees.	Spice bush	Occasional	Absent
<i>Bicuculla canadensis</i> (Goldie) Millsp.	Squirrel-corn	Common	Absent
<i>Bicuculla cucullaria</i> (L.) Millsp.	Dutchmans breeches	Common	Absent
<i>Cardamine bulbosa</i> (Schreb) B.S.P.	Bulbous bittercross	Occasional	Absent
<i>Carex cephalophora</i> Muhl.	Oval-headed sedge	Occasional	Absent
<i>Carex convoluta</i> Mack.	Convolute sedge	Common	Occasional
<i>Carex laxiculmis</i> Schw.	Spreading sedge	Occasional	Absent
<i>Carex sparganioides</i> Muhl.	Bur-reed sedge	Occasional	Absent
<i>Carpinus caroliniana</i> Walt.	Blue beech	Occasional	Occasional
<i>Castanea dentata</i> (Marsh.) Borkh.	Chestnut	Occasional	Occasional (Sprouts)
<i>Caulophyllum thalictroides</i> (L.) Mx.	Blue cohosh	Common	Occasional (Stunted)
<i>Cimicifuga racemosa</i> (L.) Nutt.	Black cohosh	Occasional	Absent
<i>Cinna arundinacea</i> (L.)	Wood reed-grass	Occasional	Occasional (Stunted)
<i>Circaea huetiana</i> L.	Common enchanters night shade	Occasional	Absent
<i>Cirsium altissimum</i> (L.) Spreng.	Tall thistle	Rare	Absent
<i>Claytonia virginica</i> L.	Spring beauty	Common	Occasional
<i>Cornus amomum</i> Mill.	Silky dogwood	Occasional	Absent
<i>Crataegus coccinea</i> L.	Scarlet thorn	Occasional	Absent
<i>Crataegus crus-galli</i> L.	Cockspur hawthorn	Occasional	Occasional (Stunted)
<i>Crataegus punctata</i> Jacq.	Dotted hawthorn	Occasional	Absent
<i>Dennstaedtia punctiloba</i> (Mx.) Moore	Boulder fern	Occasional	Absent
<i>Dentaria diphylla</i> Mx.	Two-leaf toothwort	Occasional	Absent
<i>Dentaria laciniata</i> Muhl.	Cutleaf toothwort	Common	Occasional (Stunted)
<i>Disporum lanuginosum</i> (Mx.) Nich.	Hairy disporum	Occasional	Absent
<i>Dryopteris spinulosa</i> (Muell.) Kt.	Spinulose shieldfern	Occasional	Absent
<i>Equisetum arvense</i> L.	Field horsetail	Occasional	Absent
<i>Euonymus obovatus</i> Nutt.	Running strawberry bush	Occasional	Absent
<i>Eupatorium urticaefolium</i> Reich.	White snakeroot	Occasional	Absent
<i>Erigeron bulbosa</i> (Mx.) Nutt.	Harbinger-of-spring	Common	Occasional
<i>Erigeron pulchellus</i> Mx.	Showy fleabane	Occasional	Absent
<i>Fagus grandifolia</i> Ehrh.	American beech	Occasional	Occasional
<i>Fragaria virginiana</i> Duch.	Virginia strawberry	Occasional	Occasional (Stunted)
<i>Frasera carolinensis</i> Walt.	American columbo	Rare	Absent
<i>Frazinus americana</i> L.	White ash	Occasional	Occasional
<i>Galium concinnum</i> T. and G.	Shining bedstraw	Common	Occasional
<i>Geranium maculatum</i> L.	Wild crane's bill	Common	Absent
<i>Geum canadense</i> Jacq.	White avens	Occasional	Occasional (Stunted)
<i>Glechoma hederacea</i> L.	Ground ivy	Occasional	Absent
<i>Glycine apios</i> L.	Ground nut	Occasional	Absent

TABLE 1. (Continued)

Species <sup>1</sup>	Presence and Abundance <sup>2</sup>	
	Ungrazed	Grazed
<i>Grossularia cynosbati</i> (L.) Mill.	Prickly gooseberry	Common
<i>Hepatic haptica</i> (L.) Karst.	Round-lobed liver-leaf	Occasional
<i>Hicoria cordiformis</i> (Wang.) Britt.	Bitternut	Occasional
<i>Hicoria ovata</i> (Mill.) Britt.	Hickory	Occasional
<i>Hieracium aurantiacum</i> L.	Shagbark hickory	Occasional
<i>Hydrophyllum virginianum</i> L.	Orange hawk weed	Occasional
<i>Impatiens biflora</i> Walt.	Virginia water-leaf	Common
<i>Impatiens pallida</i> Nutt.	Spotted touch-me-not	Occasional
<i>Juncoides campestris</i> (L.) Kt.	Pale touch-me-not	Occasional
<i>Juglans cinerea</i> L.	Common wood-rush	Occasional
<i>Leptanthium virginianum</i> (L.) Raf.	Butternut	Common
<i>Liriodendron tulipifera</i> L.	Beech drops	Occasional
<i>Lysias orbiculata</i> (Pursh.) Rydb.	Tulip tree	Rare (Planted)
<i>Magnolia acuminata</i> L.	Large round leaf orchid	Occasional
<i>Malus malus</i> (L.) Britt.	Cucumber magnolia	Occasional
<i>Medeola virginiana</i> L.	Common apple	Absent
<i>Mitchella repens</i> L.	Indian cucumber-root	Occasional
<i>Mitella diphylla</i> L.	Partridge berry	Occasional
<i>Nabalus altissimus</i> (L.) Hook	Two-leaf bishop's cap	Occasional
<i>Nyssa sylvatica</i> Marsh.	Tall rattlesnake root	Occasional
<i>Onoclea sensibilis</i> L.	Tupelo	Common
<i>Ostrya virginiana</i> (Mill.) Willd.	Sensitive fern	Occasional
<i>Oxalis cymosa</i> Small.	Hop-hornbeam	Common (In openings)
<i>Panax quinquefolium</i> L.	Tall yellow wood sorrel	Absent
<i>Panax trifolium</i> L.	Common ginseng	Absent
<i>Parthenocissus quinquefolia</i> (L.) Planch.	Dwarf ginseng	Absent
<i>Phlox divaricata</i> L.	Virginia creeper	Occasional
<i>Phryma leptostachya</i> L.	Wild blue phlox	Common
<i>Phytolacca americana</i> L.	Lopseed	Common
<i>Poa annua</i> L.	Pokeweed	Occasional
<i>Poa compressa</i> L.	Annual meadow grass	Occasional
<i>Poa pratensis</i> L.	Flat stemmed blue grass	Common (In openings)
<i>Poa sylvestris</i> Gr.	Kentucky blue-grass	Common
<i>Podophyllum peltatum</i> L.	Sylvan spear-grass	Occasional
<i>Polygonatum biflorum</i> (Walt.) Ell.	May apple	Occasional
<i>Polygonatum commutatum</i> (R & S) Dietr.	Hairy solomons seal	Occasional
<i>Potentilla canadensis</i> L.	Smooth sclomons seal	Common
<i>Prunella vulgaris</i> L.	Common 5-finger	Occasional
<i>Prunus virginiana</i> L.	Common self-heal	Occasional
<i>Quercus alba</i> L.	Black cherry	Occasional
<i>Quercus rubra</i> L.	White oak	Occasional
<i>Ranunculus recurvatus</i> Poir.	Red oak	Occasional
<i>Rosa virginiana</i> Mill.	Hooked crow-foot	Common
<i>Rubus allegheniensis</i> Port.	Virginia rose	Occasional
<i>Rubus occidentalis</i> L.	High blackberry	Occasional
<i>Rumex acetosella</i> L.	Black raspberry	Occasional
<i>Rumex crispus</i> L.	Sheep sorrel	Common (In openings)
<i>Sambucus canadensis</i> L.	Curled dock	Occasional
<i>Sambucus racemosa</i> L.	Common elderberry	Absent
<i>Sassafras sassafras</i> (L.) Karst.	Red elderberry	Common
<i>Smilax herbacea</i> L.	Sassafras	Occasional
<i>Solidago caesia</i> L.	Carion flower	Occasional
<i>Solidago ulmifolia</i> Muhl.	Wreath goldenrod	Occasional
<i>Synedemon thalictroides</i> (L.) Hoffm.	Flmleaf goldenrod	Absent
<i>Tiarella cordifolia</i> L.	Rue anemone	Common
<i>Tilia americana</i> L.	False miterwort	Occasional
<i>Torara virginiana</i> (L.) Raf.	American Indian Virginia knotweed	Occasional

TABLE 1. (Continued)

Species <sup>1</sup>	Presence and Abundance <sup>2</sup>	
	Ungrazed	Grazed
<i>Toxicodendron radicans</i> (L.) Kt.	Poison ivy	Occasional
<i>Tracaulon sagittatum</i> (L.) Small.	Arrow-leaf tear-thumb	Absent
<i>Trillium grandiflorum</i> (Mx.) Salisb.	Large-flowered trillium	Common
<i>Ulmus americana</i> L.	White elm	Occasional (Stunted)
<i>Ulmus fulva</i> Mx.	Slippery elm	Occasional
<i>Unifolium canadense</i> (Dest.) Greene	False lily-of-the-valley	Absent
<i>Urticastrum divaricatum</i> (L.) Kt.	Wood nettle	Common (Stunted)
<i>Urtica perfoliata</i> L.	Perfoliate bellwort	Absent
<i>Vagnera racemosa</i> (L.) Mor.	Panicled false solomons seal	Common
<i>Vagnera stellata</i> (L.) Mor.	Stellate false solomons seal	Absent
<i>Viola canadensis</i> L.	Canada violet	Occasional
<i>Viola eriocarpa</i> Schw.	Smooth yellow violet	Common
<i>Viola hastata</i> Mx.	Halberd-leaf yellow violet	Occasional
<i>Viola hirsutula</i> Brain.	Southern wood violet	Common
<i>Viola papilionacea</i> Pursh.	Common blue violet	Occasional
<i>Viola pubescens</i> Ait.	Hairy yellow violet	Absent
<i>Viola triloba</i> Schw.	Three lobed violet	Occasional
<i>Vitis cordifolia</i> Mx.	Frost grape	Occasional
TOTAL Occurring Commonly.....		25
TOTAL Occurring Occasionally.....		95
TOTAL Occurring Rarely.....		4
TOTAL Species Present.....		124
Species not Occurring in Grazed Woods		67
Species not Occurring in Ungrazed Woods.		1

<sup>1</sup>Scientific names are based on "The revised Catalog of Ohio Vascular Plants," John H. Schafner, Ohio Biol. Surv. Bull. 25, January 9, 1932.

<sup>2</sup>Common—Species which are found commonly throughout the woods or are locally abundant on suitable sites. Usually represented by a hundred or more plants.

Occasional—Species which are represented by ten to one hundred plants.

Rare—Species represented by but one to ten plants.

were probably missed because of their appearance at seasons when the areas were not visited, and several sedges and grasses have been omitted because accurate determinations are not available. The list shows that following 10 years of freedom from grazing, the ungrazed woodland has more than twice as many woodland plants as the grazed one. The greatest difference between these two areas, however, is that the plants in the ungrazed tract are more numerous and vigorous and are annually increasing, whereas in the other area they are sparse and stunted.

#### ACCUMULATION OF LEAF LITTER

Open fields border both areas on the west. It is from this direction that the prevailing winds blow. Strong southwest winds in summer and strong northwest winds in winter blow the fallen leaves to the central and eastern part of the woodlands where they accumulate. In 1932 both tracts were practically barren of leaf litter for a distance of approximately 50 yards along their western margin. Leaf litter was unevenly distributed throughout the re-

maining area. In draws and depressions and on the lee side of knolls it had accumulated 3 to 6 inches deep, while on knolls or slightly elevated areas it scarcely covered the ground.

As with natural reproduction of woody and herbaceous plants, protection did not bring an immediate change in leaf-litter accumulation. No noticeable change in its distribution took place until tree seedlings became abundant.

The leaf-fall of 1937 was the first to be partially retained in the western part of the ungrazed area. Even seedlings 4 to 6 inches in height were effective in retarding the movement of leaves by wind. In the spring of 1938, after the leaves were compacted by the winter rain and snow, depth of litter was measured in the milacre plots. Measurements were repeated in midsummer of 1942 after the litter of the previous season had partly disintegrated. In the ungrazed area the 1938 readings in undecomposed litter ranged from  $\frac{1}{4}$ -inch in the western part to  $\frac{2}{4}$  inches in the eastern part. Litter depth in the central part averaged  $\frac{2}{2}$  inches and was due to the accumulation of wind-blown leaves from many previous seasons. By 1942 the depth of partially decomposed litter had materially increased in the western part and averaged 1-inch in depth, where previously little had accumulated. Litter depth again increased progressively toward the eastern margin, where it averaged  $1\frac{3}{4}$  inches with an increase in the central part to  $2\frac{3}{4}$  inches. The outstanding feature of litter depth at the later reading was its relatively uniform distribution throughout the woodland.

In the grazed tract no observable change has occurred in litter distribution. The western fourth of the area was practically devoid of litter in 1938 and again in 1942 was too sparse for measurement. The central and eastern part had litter accumulated to an average depth in 1938 of  $1\frac{1}{2}$  inches. In the same area partially decomposed litter measured only approximately 1-inch deep in 1942.

#### POPULATIONS OF BREEDING BIRDS

Breeding bird censuses have been conducted in both tracts annually, starting with the 1938 season. The technique employed was a modification of the singing-male-count method reviewed by Lack (1937). This consisted of recording territories of singing male birds on three consecutive mornings between 5 and 9, during the Memorial Day holiday period. Each year this period corresponded with about the midpoint of bird breeding activity. These observations were supplemented by records kept during the day while other data were being obtained and by subsequent visits during the Fourth of July holiday. Records of birds observed during late March and during intermittent visits at other seasons of the year were also kept.

Frequently, nesting records were confirmed by finding nests or by observing either parent carrying food to young. This was particularly true of ground- and shrub-nesting species.

The bird-census data are summarized in Table 2. It is apparent from these that breeding birds are four times as abundant in the ungrazed as in the grazed area. The abundance of low-growing, woody, and herbaceous plants and good distribution of leaf litter in the protected woods accounts for this difference. Forty percent of the species and 60 percent of the pairs of birds found in the ungrazed area are distinctly ground and/or shrub-nesting species. By contrast, only 27 percent of the species and 27 percent of the pairs in the grazed area are ground and/or shrub-nesters. These include yellow-billed cuckoo, ovenbird, redstart, towhee, bobwhite, indigo bunting, song sparrow, vesper sparrow, and field sparrow. Two other species, the yellow-throated vireo and red-eyed vireo, have nested in the more vigorous seedlings and a third, the cowbird, frequently lays its eggs in nests of ground- or shrub-nesting birds. Four species, crested flycatcher, chickadee, tufted titmouse, and white-breasted nuthatch, are hole nesters; phoebes utilized the sugar house; and the others nested in the branches of the large trees.

The number of pairs and species present has varied from year to year. Since an unexplained low of 126 pairs of birds to the hundred acres in the protected tract in 1939, there has been a substantial gain in this area each year. Slight gains also have been recorded in the grazed area. The gain recorded may be due in part to increased skill in recording singing males. The material increase in the ungrazed area, however, is believed to be due to an increasingly varied habitat provided by seedling trees, shrubs, and herbaceous plants.

#### POPULATIONS OF MAMMALS

An apparent increase in abundance of mammals paralleled the development of new woody growth and better distribution of leaf litter in the ungrazed woods. In 1941, the beginning of an upswing in the mouse cycle, pine mouse, and short-tailed shrew runways were abundant under leaf litter throughout this area. Runways occurred much less frequently in the grazed tract where the absence of litter and of food appeared to be the limiting factors. To determine the relative populations of small mammals in the areas, two  $\frac{1}{10}$ -acre quadrats were trapped out in each tract during the week of December 20, 1941. The trapping method followed was patterned after the system used by Boles (1939) and his coworkers.

One area in the eastern part and one in the western part of each tract was selected for trapping. A line was made through the middle of each tract from north to south. Diagonal lines were run across the resulting blocks and the point where they met was selected as the center of each quadrat. The quadrats were laid out one chain square and marked with wire stakes. Sixty-four ordinary snap-back mouse traps were allotted for each quadrat, and an additional 20 traps were used to provide a buffer around them one rod from the perimeter. The traps were baited with dried seedless raisins and set in frequently used run-

TABLE 2. Population of breeding birds—1938-1942.

Species Nesting and Feeding in Woodland	Ungrazed Woodland							Grazed Woodland						
	1938	1939	1940	1941	1942	5- year total	5- year ave.	1938	1939	1940	1941	1942	5- year total	5- year ave.
Yellow-billed cuckoo ( <i>Coccyzus americanus americanus</i> L.)	1				1	2	0.4							
Ruby-throated hummingbird ( <i>Archilochus colubris</i> L.)					1	1	0.2							
Downy woodpecker ( <i>Dryobates pubescens medianus</i> Swainson)				1	1	2	0.4							
Crested flycatcher ( <i>Myiarchus crinitus boreus</i> Bangs)		1				1	0.2							
Phoebe ( <i>Sayornis phoebe</i> Latham)					1	1	0.2							
Wood Pewee ( <i>Myiochanes virens</i> L.)	1	1	1	1	1	5	1.0					1	1	0.2
Black-capped chickadee ( <i>Penthestes atricapillus atricapillus</i> L.)	1					1	0.2							
Tufted titmouse ( <i>Baeolophus bicolor</i> L.)	1			1	1	3	0.6				1	1	2	0.4
White-breasted nuthatch ( <i>Sitta carolinensis carolinensis</i> Latham)											1		1	0.2
Eastern robin ( <i>Turdus migratorius migratorius</i> L.)				1	1	2	0.4	1				1	2	0.4
Yellow-throated vireo ( <i>Vireo flavifrons</i> Vieillot)			1		1	2	0.4					1	1	0.2
Red-eyed vireo ( <i>Vireo olivaceus</i> L.)	2	1	2	2	2	9	1.8	3	2	2	2	2	11	2.2
Cerulean warbler ( <i>Dendroica cerulea</i> Wilson)	1				1	2	0.4							
Ovenbird ( <i>Seiurus aurocapillus</i> L.)	2	2	2	2	2	10	2.0	2	1	1	1	1	6	1.2
Am. Redstart ( <i>Setophaga ruticilla</i> L.)	1			1	2	4	0.8							
E. cowbird ( <i>Molothrus ater ater</i> Boddaert)				1	1	2	0.4							
Indigo bunting ( <i>Passerina cyanea</i> L.)									1				1	0.2
Red-eyed towhee ( <i>Pipilo erythrophthalmus erythrophthalmus</i> L.)					1	1	0.2							
Species Nesting in Woods, but Feeding all or partially outside of the woods:														
E. Bobwhite ( <i>Colinus virginianus virginianus</i> L.)	0.5					0.5	0.1							
E. crow ( <i>Corvus brachyrhynchos brachyrhynchos</i> Brehm)				1		1	0.2				1		1	0.2
Scarlet tanager ( <i>Piranga erythromelas</i> Vieillot)												1	1	0.2
Indigo bunting ( <i>Passerina cyanea</i> L.)	2		2	2	1	7	1.4							
E. vesper sparrow ( <i>Poocetes gramineus gramineus</i> Gmelin)		2				2	0.4							
E. field sparrow ( <i>Spizella pusilla pusilla</i> Wilson)	1	1	3	2	2	9	1.8		1		1		2	0.4
M. song sparrow ( <i>Melospiza melodia beatal</i> Bangs)	2	2	1	2	1	8	1.6							
Total species	12	7	7	12	17	22	11	3	4	2	6	7	11	4.2
Total pairs	15.5	10	12	17	21	75.5	15.1	6	5	3	7	8	29	5.8
Total pairs per 100 acres	197	126	152	216	265	948.5	189.7	47	40	24	56	63	230	46.0

ways and all likely looking places such as the base of stumps. The traps were set an average of 8 feet apart each way, but no special effort was made to keep the distance uniform. Where small mammal signs warranted it, several traps were set close together, while in barren places traps were set farther apart. All traps were covered with 1-foot square heavy tar paper covers. Traps in each plot were visited early in the morning after each of three consecutive nights of trapping.

The number and size of samples taken was necessarily small. The results indicate, nevertheless, that

little quantitative difference existed between small mammal populations in the eastern part of the ungrazed and the grazed woodlands where leaf litter was of similar depth. Actually, in these plots the grazed area had a slightly higher population. Where leaf litter was sparse, as in the western part of the grazed tract, a marked quantitative difference occurred. In these plots small mammals were found to be three and one-third times more abundant in the ungrazed than in the grazed tract. The small number of shrews and absence of pine mice in the grazed tract accounts for this difference (Table 3).



TABLE 3. Small mammals collected in 0.1 acre quadrats, sugar maple woodland, grazed and ungrazed.

		Plots in Western part		Plots in Eastern part		Total caught	Total per acre
		Number	Per acre	Number	Per acre		
Short-tailed shrew ( <i>Blarina brevicauda</i> kirtlandi Bole and Moulthrop)	Ungrazed	6	60	3	30	9	45
	Grazed	1	10	4	40	5	25
White-footed mouse ( <i>Peromyscus leucopus noveboracensis</i> Fischer)	Ungrazed	1	10	1	10	2	10
	Grazed	2	20	2	20	4	20
Pine mouse ( <i>Pitymys pine-lorum scalopsoides</i> Aud. and Bach.)	Ungrazed	3	30	1	10	4	20
	Grazed	0	0	0	0	0	0
Total.....	Ungrazed	10	100	5	50	15	75
	Grazed	3	30	6	60	9	45

No pine mice were taken in either of the two plots in the grazed woodland. Their low population, or absence, is believed due to lack of litter suitable for feeding runways and to lack of new woody and herbaceous plants necessary for food. All of the shrews found in the grazed tract were taken in runways in the loose litter at the base of rotting tree stumps. Many more stumps occur in this area than in the other on account of recent cutting operations and because the owner of the ungrazed woodland utilizes his stumps for fuel. The greater number of stumps in the grazed tract probably also accounts for the somewhat higher population of white-footed mice recorded there.

In addition to the three species taken in the quadrats, at least 11 other small mammals have been recorded in this study. Opossums are known to be present in both woodlands from tracks found in the snow. Occasionally one is found at the base of a hollow tree by dogs or when trees are felled for fuel. Hairy-tailed moles have numerous runways in the ungrazed and occasional runways in the grazed areas. Raccoons are known to forage in both tracts but probably do not den in either area. The common skunk is a permanent resident of both areas. It utilizes woodchuck dens, and dens annually under the sugar house woodshed in the ungrazed tract. A red fox was observed in the ungrazed woodland December 24, 1941. Tracks in the snow indicate that it has an established hunting route through this area. No fox tracks have been observed in the grazed area.

Woodchucks are very abundant in the grazed area. They seem to be favored by the sunlit openings and large decadent stumps under which they dig their burrows. Six occupied sets of burrows were recorded in the summer of 1942 in this woodland. All of them were in well-drained, sunny locations within 75 yards of the woodland boundary. Three sets of burrows were found in the ungrazed tract. Of these, one was under the sugar house, another under a fuel wood pile, and the third in a sunlit opening in the

eastern part of the woodland made by a recent wind-fallen tree. The more dense shade, higher humidity, and greater percent of heavy soil of the ungrazed tract does not appear to be as favorable to the woodchuck as conditions in the other woodland.

Eastern chipmunks appear to be more abundant in the ungrazed tract. This observation, however, may be due to the fact that they can be more closely approached and thus heard more readily there, and to the fact that there are two stone piles in this tract which appear to be favored habitats. Red squirrels have occasionally been noted in both woodlands. Fox squirrels are present but not abundant in either area. The absence of suitable large den trees and nut-producing trees is the factor limiting their abundance. The importance of food was illustrated by the appearance of 5 leaf nests of this squirrel in the ungrazed woods after the pasture field to the north was plowed and planted to corn. Apparently their occupants moved in from the adjacent woodlands and remained as long as the food supply was available.

Flying squirrels are present in both tracts. No observations have been made as to their relative abundance. Their presence is known by the invariable experience of finding one or more drowned in a sap bucket each spring. Presumably, they fall into the bucket while trying either to obtain a drink or to catch the male spring canker worm moths (*Paleacrita vernata* Peck), which frequent the sap buckets near the close of the sugaring season.

Cottontail rabbits have increased materially in the ungrazed woodland. In the spring of 1942, after four had been shot during the preceding winter, their number was estimated to be about one to the acre. During the winter months they girdled hundreds of young trees that were under one inch in diameter. In several dense colonies of young maples approximately 85 percent of the young trees were injured to some extent. This has probably been beneficial by thinning these dense stands thus reducing crowding. Unfortunately, however, the larger saplings are also often injured. Cottontails are seldom observed in the grazed woodland and when jumped there they immediately seek the cover of the ungrazed area.

Possibly other small mammals appear occasionally in these two tracts but have escaped notice because of their infrequency or secretive habits. An accurate census of the 14 species known to occur was not made, but it is believed that the estimate given in Table 4 is a fair minimum approximation of the numbers present in May 1942.

#### POPULATIONS OF INVERTEBRATES

To determine the relative abundance of litter-inhabiting invertebrates, 10 individual square-foot leaf-litter samples were taken in each area December 24, 1941. All of the litter and the humus layer enclosed within a square-foot metal frame was collected and placed in an individual close-knit cloth

TABLE 4. Estimated relative abundance of mammals.\*

Species	Ungrazed Woodland		Grazed Woodland	
	Number	Number per acre	Number	Number per acre
Opossum ( <i>Didelphis virginiana virginiana</i> Kerr)	2	0.25	4	0.33
Hairy-tailed mole ( <i>Parascalops breweri</i> Bach.)	8	1.00	6	0.50
Short-tailed shrew ( <i>Blarina brevicauda kirtlandi</i> Bole and Moulthrop)	355	45.00	310	25.00
Raccoon ( <i>Procyon lotor lotor</i> L.)	visi	tor	visi	tor
Skunk ( <i>Mephitis mephitis nigra</i> Peale and Beauvois)	4	0.50	4	0.33
Red Fox ( <i>Vulpes fulva fulva</i> Desmarest)	visi	tor	no	record
Woodchuck ( <i>Marmota monax rufescens</i> Howell)	6	0.75	12	1.00
Chipmunk ( <i>Tamias striatus rufescens</i> Bole and Moulthrop)	8	1.00	8	0.75
Red Squirrel ( <i>Sciurus hudsonicus loquax</i> Bangs)	2	0.25	4	0.33
Fox squirrel ( <i>Sciurus niger rufiventer</i> Geoff.)	6	0.75	4	0.33
Flying squirrel ( <i>Glaucomys volans volans</i> L.)	6	0.75	8	0.75
White-footed mouse ( <i>Peromyscus leucopus noveboracensis</i> Fischer)	79	10.00	248	20.00
Fine mouse ( <i>Pitymys pinetorum scalopoides</i> Aud. and Bach.)	158	20.00	no	record
Cotton-tail rabbit ( <i>Sylvilagus floridanus mearnsi</i> Allen)	8	1.00	visi	tor
Total	642	81.20	608	49.00

\*Bole 1942.

bag. The material collected was stored at room temperature for 24 hours. Each sample was then run through a Berlese funnel to which was added two drops of chloropierin to activate the invertebrates

and cause them to fall through a screen into a receptacle. The material forced out of the litter by this procedure was then carefully worked over under a strong light and all organisms large enough to be detected with the naked eye were collected and saved for identification. As a further check, the litter was also examined after removal from the Berlese funnel. A tabulation of the material collected is presented in Figure 9.

The number of invertebrates found in the ungrazed tract, 2,234,000 per acre was more than two and one-half times the number, 810,000 per acre, found in the grazed area. More than 60 percent of these organisms (Diplopoda, Chilopoda, Nematoda, Coleoptera, Diptera, Collembola, Corrodentia, and Annelida) are commonly found associated with decomposing plant material upon which some of them may feed. The other invertebrates present, including some of the Coleoptera and Diptera, were the overwintering stages of phytophagous or predaceous species.

At least three factors are believed to be primary underlying causes of the marked difference in populations. The most obvious fact is that there is less leaf litter in the grazed tract. There also is less green leaf surface of low-growing plants on which invertebrates feed in the summer before hibernating beneath the dead leaves. Another important factor is the relative stability of the litter. In the grazed tract the litter is constantly being shifted by variation in the velocity and source of the wind. Under these

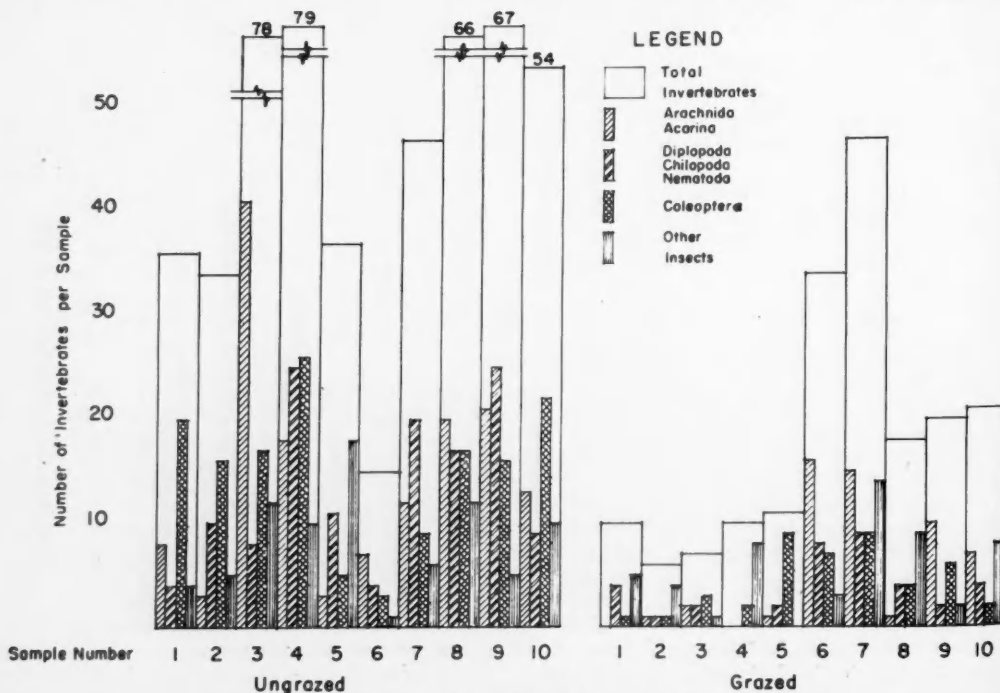


Fig. 9. Invertebrate populations in leaf litter collected in winter.

conditions the litter and the soil under it become too dry for suitable hibernating quarters for most invertebrates. Further, many organisms which do hibernate are later exposed to their enemies and the elements by movement of the litter.

The relative abundance of invertebrates found in litter in various parts of the two woodlands is illustrated by the data shown in Figure 9. The samples were numbered progressively from 1 to 10 as they were taken at random along a diagonal route from the northwest to the southeast corners of each tract. Thus, the first sample in each area is representative of the most severely grazed portions and the last sample is representative of the least severely grazed condition. The first two samples in the ungrazed tract are of leaf litter accumulated since elimination of grazing. The third and fourth are from an area of litter accumulation in a slight depression. The next three are from a wind exposed knoll, and the last three are from the part of the woodland least disturbed by grazing prior to removal of the livestock. Invertebrate populations change directly with the changes in litter depth. This is even more clearly illustrated in the grazed woodland material. The first 5 samples from this area were taken in the wind-swept western part. The next two are from the zone of litter accumulation and the last three from the zone where litter has been disturbed the least by grazing.

#### PHYSICAL AND ECONOMIC FACTORS

The data presented thus far are evidence that protection from grazing had made possible a material increase in the abundance of plants and animals in the ungrazed woodland. They do not seem adequate, however, to explain the fact that the ungrazed tract, under nearly identical management, except for grazing, has yielded approximately one-fourth more maple syrup a year than the grazed tract.

In an effort to find some tangible factor to which this difference could be attributed, a number of measurements were made of soil characteristics. The first measurements were of soil moisture present at one and two foot depths. One set of samples was obtained December 26, 1941, and another March 9, 1942, during the syrup-making season. Approximately 150 to 200 grams of soil were collected for each sample and placed in small metal soil cans. The cans were sealed with cellulose tape. Percent of moisture was determined in the laboratory as that part of the weight of the sample lost by drying in an oven at 100 degrees C. for 24 hours.

The December studies included 6 samples from each depth in both woodlands. In March 4 sets of samples were taken in the ungrazed area and 6 sets in the grazed area. Samples were taken at random along a northwest to southeast route in both areas.

The data show that only a slight difference in moisture content occurs between the two areas (Table 5). They also show that no substantial change in moisture content occurred during the winter months.

The percent of moisture recorded is probably lower than the mean for the soil types because of a rainfall deficiency during the preceding 12 months.

TABLE 5. Moisture content of soil in grazed and ungrazed woodland.

	Ungrazed Tract		Grazed Tract	
	December 1941	March 1942	December 1941	March 1942
Average percentage of moisture one foot deep.....	17.5	17.0	17.1	16.7
Average percentage of moisture two feet deep.....	15.3	15.5	15.1	14.4

Core samples at the surface and at 6-inch depths were taken in March, 1942, at the same time and place as the soil moisture samples. Brass cylinders 3 inches long and 1½ inches in diameter were used to obtain the cores. They were forced into the ground by steady pressure on a driving head and lifted out carefully with a shovel. The soil which protruded from the lower end, was pared off with a knife and the ends sealed with a metal disk and wrapped with cellulose tape. Samples were not obtained in the extreme western part of the grazed tract because the ground there was frozen hard. No frost was present in the eastern part of this tract nor in any part of the ungrazed woodland. The ground in the latter area was so thoroughly undermined with small mammal runways that numerous trials were necessary to obtain unbroken soil columns. This may have resulted in selection of samples which were heavier than average. Air temperatures at this time ranged between 34° and 40° F.

A practical procedure for soil analysis developed by R. W. Gerdel was used. The soil-filled cylinders were soaked overnight in distilled water, weighed after draining off excess water, and then placed right side up on a moist blotter over a screen in a compartment designed to maintain high humidity. To determine percolation rate, a 2-inch high, water-tight, rubber collar was placed on the upper end of each core and a point indicator fastened to the collar. Distilled water was then added to the level of the point indicator, the time to the nearest one second noted, and, after the water had gone down a measurable distance, the collar was refilled to the point indicator from a burette and the time noted again. In this manner it was possible to obtain the rate in cc. per second of percolation through saturated soil under relatively constant humidity and pressure.

After percolation rates were determined the soil was allowed to air-dry until a reading of pF 1.78 was obtained by use of a potentiometer. The weight of the soil at this reading was considered weight at the approximate wilting coefficient. The oven-dry weight of the cylinder and soil, and the tare weight and volume of the empty cylinders, were then determined. These calculations were made to determine volume weight, capillary and non-capillary porosity and total porosity of the soil (Table 6).

The volume weight of soil at the surface and at the 6-inch depths was slightly higher in the ungrazed tract which indicates a somewhat heavier, more impervious condition. Surface percolation or infiltration rate, however, was noticeably greater than in the grazed area. Percolation below the 6-inch depth is very slow in both tracts, but averages slightly higher in the grazed tract. Non-capillary or air capacity of surface samples was distinctly higher in the ungrazed area, but samples at the 6-inch depth are much lower than those in the grazed tract at the same depth. In both tracts, non-capillary capacity below the 6-inch depth is too low for satisfactory plant development.

According to Chadwick (1941) "a well-aerated soil should contain over 10 percent of large pores on the basis of the total soil volume" for satisfactory hardwood root development. "If there are less than 10 percent, root growth is not normal." On this basis conditions are unfavorable for best root growth in both tracts. The soil in the ungrazed area, however, with the average of 8.9 percent of air space in the upper 6 inches, is decidedly more favorable for root growth than that in the grazed area, where only 6.9 percent of the total volume is represented by air space. In view of the past history of the ungrazed tract and the fact that it has a relatively higher proportion of heavy soil, it is very probable that the air space has increased since grazing was eliminated. Increased air capacity and percolation rate are probably the result of leaf litter accumulation and its incorporation into the soil by the process of decay and the activity of soil inhabiting mammals and invertebrates.

There is very little difference in the capillary porosity of soils in the two tracts. This is also true for the total water-holding capacity of the soil, which amounts to approximately 50 percent by volume in the surface soil and 40 percent by volume in the subsoil (Table 6).

TABLE 6. Soil factors.

	Ungrazed Tract		Grazed Tract	
	Surface cores	6 in. cores	Surface cores	6 in. cores
Average percolation rate—cubic inches per hour.....	3.14	0.08	2.59	0.11
Average volume weight of soil—gms. per cc.....	1.12	1.58	1.07	1.46
Average percent by volume—non-capillary porosity.....	8.89	3.41	6.86	5.08
Average percent by volume—capillary porosity.....	41.65	37.08	43.65	36.33
Average percent total porosity or water holding capacity....	50.54	40.49	50.51	41.87

These data while not adequate to account for the difference in syrup production between the two tracts, do show physical differences in the soil that affect plant growth. Of possibly greater importance is the fact that freezing of the soil is much less severe and retention of snow is much greater in the ungrazed than in the grazed tract. In late February of 1940, for example, following an extended "cold snap"

(minimum temperature of 16° F. below zero) the ungrazed area had a rather uniform mantle of snow 8 to 12 inches deep whereas the western margin of the grazed area was swept nearly bare of snow for a distance of 50 to 75 yards. The ground was not frozen in the ungrazed woods at this time, but in the grazed area it was frozen to a mean depth of 4.5 inches along the exposed western part. The operator of the maple syrup camp in the grazed tract has noted that trees in this part of his woodland are not so productive as trees of comparable size in the eastern part where conditions are more typical of protected forests. The owner of the ungrazed tract, on the other hand, has reported a notable increase in flow of maple sap in the western part of his woodland.

## DISCUSSION

The data obtained in this study confirm the general observation of many conservationists that woodland protected from injury by grazing has a much richer flora and fauna than does grazed woodland of similar composition. Of even more importance, the study shows that a severely grazed woodland can become rejuvenated within a reasonably short time after protection is provided. Rejuvenation in this case was made possible by a rapidly changing inter-related series of biologic events. The most important of these is the influence of man in removing the livestock which brought about decline of the woodland.

An abundant seed crop and weather favorable for seed germination within a few years was the next major event in the rejuvenation process. The developing seedlings provided conditions suitable for the events which followed. Their retarding influence on drying winds and the improvement in leaf litter distribution made it possible for other kinds of plants to grow.

Concurrent with improvement of the plant and litter cover, animal populations became larger and more varied. The birds that utilized the leaf litter and seedling trees as nesting cover probably fed on the insects which fed on the young trees and also probably brought seeds of additional plants into the woodland. Small mammals like shrews and pine mice found an abundance of food in the plant-feeding invertebrates and the underground stems of the thousands of new plants. The runways, burrows, and food caches they made have helped to aerate the soil and bring many plant seeds in contact with mineral soil, which is essential for their development. Rabbits and pine mice reduced density of stands by girdling seedlings and saplings where they grew in thick clumps, thus making it possible for the uninjured trees to grow more rapidly.

The invertebrates which inhabited and fed on the litter, such as millipedes, and earthworms, probably helped to change it to duff and humus. Their burrows and feeding tunnels probably also improved the aeration of the soil. That some plants would develop without the increased activity of these animals is



evident from the initial growth of seedling maples before there was evidence of increased animal populations. Many heavy-seeded plants, however, like the hickories, spice bush, sassafras, ginseng, elderberry, cohosh, Solomon's seal, and Jack-in-the-pulpit, could have been transported to the woodland and planted in mineral soil only by animals. The vigor of many of these plants, too, is dependent upon the loosening and aeration of the soil. It is thus evident that, although the animals are entirely dependent upon the plants, they may to some extent contribute to the abundance, vigor, and variety of plant growth.

The knowledge that these interrelationships are essential to the best growth of a forest is of practical value to the farmer who is interested in getting the maximum return from his woodland. It also should be of considerable importance to the conservationist who is trying to improve soil and water conditions by encouraging farmers to exclude livestock from their woodlots. With these facts in mind, he can point out to the farmer, not only that grazing injures a woodland but how it injures it and how a seriously grazed woodland can be restored by protection alone.

The data presented are from a single pair of woodlots representative of one forest type and one management system. It is unlikely that identical results would be obtained from elimination of grazing in other grazed wooded areas because of the great variation that exists in forest management and ecological conditions. General observations in many farm woodlands in the Ohio Valley, however, lead the writer to conclude that the same general pattern of forest restoration would occur wherever grazed beech-maple woodlands are subsequently protected from further grazing.

The abundance, variety, and vigor of forest plants and animals will invariably be greater in woodland from which livestock are excluded than from comparable grazed areas. Studies previously reported by Chandler (1940), (1932), Dambach & Good (1940), Den Uyl (1938), Diller (1937), and others substantiate this view. Local economy and appreciation of aesthetic values will determine whether or not providing protection from grazing is worth the price to the individual. The data obtained in this and in a Maryland study (Huffman 1940) and in a recent report by Sears (1943) indicate that protection from grazing does result in substantially greater returns in woodlands operated as sugar maple camps. In this study the average yearly gross cash receipts from the sale of maple products at comparable prices has been \$43.94 per acre from the ungrazed tract as compared to \$33.27 from the grazed tract during the five-year period (1938-1942). This significant difference of \$10.67 per acre per year means an annual loss in potential income of \$132.31 to the owner of the grazed woodland. Under less intensive management, and with lower value products, however, the returns would obviously be proportionately lower.

## SUMMARY

A study was made of the development of the flora and fauna and of the economic returns from a formerly severely grazed sugar maple woodlot in Geauga County, Ohio, during the ten-year period immediately following discontinuance of grazing. The study included collection of comparative data from an adjacent grazed woodlot of similar composition and under similar management.

At the time the study was started both areas had been so severely grazed that young seedling trees were unable to become established and only a relatively few stunted herbaceous plants could be found.

Seedling trees first became established in large numbers in the ungrazed woodland the third growing season subsequent to their protection from grazing. Their number increased rapidly and attained an average abundance of nearly 80,000 per acre by the middle of the eighth growing season. Sugar maple comprised between 96 and 99 percent of the stand at all times. Eighteen other species of trees including tulip poplar, white ash, and red and white oak also appeared. Except for an occasional tulip poplar and a number of planted white ash the recent sugar maple trees have outgrown all other species. In the adjacent grazed woodland no seedling trees have become established despite the germination there each year of thousands of tree seeds.

The development of herbaceous and shrub species has followed a similar pattern. At the end of the 10-year period, 124 kinds of vascular plants were found in the ungrazed as compared to 61 in the grazed tract. The latter are for the most part sparsely represented and stunted in growth. In the ungrazed tract many of the species are abundant and thrifty in appearance.

A notable improvement in the accumulation and distribution of leaf litter has taken place in the ungrazed area. Additional leaf litter apparently is added by the developing woody and herbaceous plants and their numerous upright stems materially reduce leaf movement by wind action. This has resulted in a rather uniform covering of leaves throughout the woodland as contrasted with the appearance of a large uncovered area in the western part previous to elimination of grazing. In the grazed tract litter has not increased appreciably and leaves from the western part of the woodland are blown into the interior and eastern part.

Annual censuses of breeding birds for a five-year period indicate that they are four times more abundant in the ungrazed as in the grazed woodland and that the ungrazed area is host to twice as many species. Forty percent of the species and 60 percent of the pairs of breeding birds in the ungrazed area are ground or shrub nesting species as contrasted with but 27 percent of the species and the same proportion of pairs (27 percent) in the grazed area.

Mammal populations show a somewhat similar correlation. It was estimated that there were 81 mammals per acre in the ungrazed as compared to

49 per acre in the grazed woodland at the close of the study period. All of the 14 species recorded occurred in the ungrazed area as contrasted to 12 in the grazed area. Ten species were equally or more abundant in the ungrazed area. Red squirrels, and white-footed mice, opossum and woodchucks were somewhat more abundant in the grazed area. Differences in soil and the number of stumps probably accounts for the greater abundance of opossum, woodchucks, and white-footed mice.

Overwintering invertebrates were found to be two and a half times more abundant in leaf litter collected at random in the ungrazed as from litter collected in the grazed tract. Abundance of invertebrates was closely associated with depth and stability of litter. The deep and relatively stable litter had the greatest numbers whereas shallow, frequently disturbed litter had small numbers of invertebrates.

Soil samples collected and tested during the winter months revealed no significant differences in moisture content from samples collected at 1- and 2-foot depths. The rate of water percolation and the percentage of total volume represented by air space were significantly greater, however, in surface cores from the ungrazed as compared to those from the grazed tract. In addition freezing of the mineral soil was not observed in the ungrazed area at a time when the soil in the exposed western part of grazed area was frozen to an average depth of 4.5 inches.

The average yearly income from the sale of maple products is \$10.67 more per acre in the ungrazed than in the grazed tract at comparable prices. This material difference in productiveness cannot be wholly explained by the data obtained in this study. The data do show, however, that elimination of grazing has resulted in distinct changes in the flora and fauna of the woodland and also of the litter and to some extent soil conditions. The sum total of these changes together with unrecorded factors may account for the favorable economic returns accompanying the discontinuance of grazing.

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ECOLOGIC RELATIONS AND ADAPTATIONS OF THE  
LIMBLESS LIZARDS OF THE GENUS ANNIELLA

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# ECOLOGIC RELATIONS AND ADAPTATIONS OF THE LIMBLESS LIZARDS OF THE GENUS ANNIELLA

## INTRODUCTION

The purpose of this study of the limbless lizards of the genus *Anniella* is to assemble all that is known about the ecology and the mode of life of these fossorial animals. The area in which special work was conducted included the northern end of the range of *Anniella pulchra pulchra* and most of the known range of *Anniella pulchra nigra*. Emphasis has been placed on the ecology of *A. p. nigra* because of the greater abundance of individuals of this race. The restriction of my activities to the northern part of the range of the genus limited observations to two climatic regions, the central coastal and northern San Joaquin Valley areas of California.

Twenty examples of *A. p. pulchra* have been taken by me at Antioch, California, and 109 examples of *A. p. nigra* on the Monterey Peninsula; 100 of these lizards were kept alive in the laboratory at Berkeley, some of them for more than a year. In addition I have examined 142 specimens: 23 *pulchra* and 21 *nigra* in the collection of the Museum of Vertebrate Zoology, and 50 *pulchra*, 46 *nigra*, and 2 *A. geronimensis* in the collection of the California Academy of Sciences.

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## METHODS

Wherever an *Anniella* was found, the temperature of the sand at the spot was recorded and a sample of the soil was placed in a stoppered glass vial. These samples were dried in an oven at 100° C. to determine the moisture content. Forty selected samples were then burned in an electric muffle at 650° C. for approximately one and one-half hours to determine the organic content.

On collection, each live lizard was marked and the progress of shedding and growth was recorded. The mark was a tattoo which was made by the use of a hypodermic needle and Higgins eternal black ink. The ink was introduced just under the skin on the venter of the lizards; thus a pattern of dark spots was made.

At Point Pinos, Monterey County, *A. p. nigra* occurs naturally on a small island which is cut off

from the mainland by the tidal zone. The lizards cannot migrate from the island to the mainland because of the barrier formed by the tidal zone. Because this population is isolated and can in no way become mixed with that on the mainland except through the agency of man, this island was chosen as the site of an experiment on mixture of populations. In September, 1940, 10 *A. p. pulchra* (all marked individually) were planted on the island which has a known population of 45 *A. p. nigra* (probably only a small proportion of the total population). It is my hope that herpetologists, who are practically the only people who know of the lizards' presence there, will spare the population from further depletion until after twenty or thirty years, which I judge to be sufficient time for the two races to intermix thoroughly. The *A. p. pulchra* so planted were all taken from Antioch, Contra Costa County.

The coast line of Point Pinos is being altered by the sea. Probably within the next hundred years this island will be reduced to a pile of bare granite rocks and the sea will end the experiment.

In the examination of specimens the following measurements were taken:

*Snout-vent* (SV), tip of snout to posterior limit of anterior margin of vent, on ventral surface.

*Tail length* (TL), posterior limit of anterior margin of vent to tip of tail.

*Regenerated portion of tail*, most anterior sign of break to tip of regenerated cone.

*Snout-orbit* (SO), posterior extremity of first preocular to tip of snout.

*Mouth length* (M), posterior side of sixth supralabial to tip of snout.

*Interorbital width* (IO), dorsal head width measured between the first supraoculars.

## THE TAXONOMIC STATUS OF THE GENUS

The genus *Anniella* was described in 1852 by Dr. J. A. Gray (p. 440) who placed it in the family Scincidae near *Soridia* in the tribe Siaphosinae. He remarked that "this is the only genus of the tribe yet found out of Australia." That the genus *Anniella* constitutes a distinct monogeneric family, *Anniellidae* (Cope 1864), and is most closely related to the *Anguidae* from which it has degenerated, is a view now generally accepted. The degenerative relationship was first pointed out by Boulenger in 1884 (pp. 120-121) and was upheld by Baur (1894: 348) and Camp (1923: 297). Camp states that the "*Anniellidae* are close to *Gerrhonotus* in structure of throat muscles and hemipenes." Further he regards (p. 418) the *Anniellidae* as a branch of the

Anguidae and thinks that (p. 333) the two families probably separated in the Upper Miocene.

The genus *Anniella* includes two species, one of which has two subspecies. *Anniella pulchra* is the type species described by Gray in 1852. *Anniella nigra* was described by Fischer in 1885. Intergrades connecting these two forms are found at Morro Bay and Pismo in San Luis Obispo County, California (Grinnell & Camp 1917; Klauber 1940) and at the mouth of the Salinas River on the shore of Monterey Bay, Monterey County (Miller 1943); thus they are reduced to subspecific rank as *Anniella pulchra pulchra* and *Anniella pulchra nigra*.



FIG. 1. *Anniella pulchra pulchra* (silvery limbless lizard), left, and *Anniella pulchra nigra* (black limbless lizard). Photographed alive, about natural size.

*Anniella geronimensis* was described by Shaw (1940) from San Geronimo Island, Lower California, Mexico.

### LIFE HISTORY

#### FOOD

The limbless lizards are predaceous, feeding largely on insect larvae, adult beetles, and other small insects and spiders. Van Denburgh (1897: 119; 1922: 470) reports *A. p. nigra* feeding on "large insect

larvae (more than 1¼ inches long), and two small ground dwelling beetles (*Helops* and *Platydemus*)."

Laboratory animals were fed on larvae of grain beetles (*Tenebrio molitor*) and termites (*Zootermopsis* sp.). Sickness and death of lizards apparently from vitamin D deficiency were overcome by feeding the termites on filter paper dampened with vitamin concentrate (B<sub>1</sub> and D).

Captive lizards were quite agile in pursuing the termites, but they rarely came out of the sand farther than half the body length. After catching the prey, the lizard would back down the burrow and sometimes devour the termite under the surface. In swallowing, the lizard chews and gulps, sometimes pushing the termite against the sand to get a better grip. In this way much sand is swallowed with the food. The head sways from side to side while chewing. Termites were swallowed quickly but a large beetle larva sometimes required several minutes to be eaten. After swallowing, the lizard "licks its chops" for several seconds.

The feces of *Anniella* are typically lacertilian with a small, hard, white chalk-like oval mass and a loose unevenly shaped mass of moist undigested insect parts. Occasionally when a lizard is handled, live nematodes and cestode proglottids are extruded with the feces, as are several drops of clear watery liquid.

#### OVULATION

The breeding cycle discussed here applies to *A. p. nigra* unless otherwise specified. Ovulation occurs in May, June or July. The earliest record of an ovum in the oviduct was on May 21. Two lizards in the laboratory had ovulated by June 9, and two by June 26.

Fourteen ova (both fertile and infertile) taken from oviducts of preserved lizards averaged 23.6 mm. (16.2 to 30.3 mm.) in length and 4.9 mm. (3.3 to 6.7 mm.) in width. The number of ova present in the oviduct at one time was found in eight lizards to vary from one to four (averaging 1.7).

Anomalies in ovulation or failure to abort unfertilized ova account for the presence of hard dried yolk in the oviduct of one individual in March and in one *A. p. pulchra* in September.

#### DEVELOPMENT

If insemination occurs before ovulation, the ova will be fertilized in the order of their entry into the oviduct, thus two embryos taken from the same female will be in slightly different stages of development. If copulation occurs after ovulation, the embryos will all be in the same stage of development. Both conditions were found in females killed on August 6, 1939. In one female the embryos were 22.9 and 28.3 mm. SV, while in another they were 23.0 and 23.6 mm. SV (Table 1).

The smallest embryos examined were taken from a female which had been killed on July 17. These two embryos were tightly coiled and it was impossible to straighten them without breaking the brittle tis-

TABLE 1. Measurements of sample embryonic, immature and adult *A. p. nigra*, showing the changes in body proportions throughout life; x indicates a broken tail; \* indicates an approximate date.

Date killed	Sex	SV	Total	Tail	SO	M	H	IO	
July 18	—	—	—	—	—	—	—	—	Curled 4.5 x 3.8 mm.
August 7	—	—	17.9	—	.7	—	—	—	Curled 5.3 x 4.5 mm.
July 3	—	12.0	18.0	6.0	—	—	3.2	—	
August 6	—	23.0	31.2	8.2	1.5	2.8	—	1.3	Same parent
August 6	—	23.6	32.1	8.5	1.5	2.7	—	1.3	
August 6	—	22.9	31.7	8.8	1.4	2.5	—	.8	Same parent
August 6	—	28.3	36.9	8.6	1.8	3.4	—	.9	
October 10*	—	29.0	40.1	11.1	1.8	—	—	—	Aborted
August 6	—	29.2	40.3	11.1	1.8	3.0	—	1.5	
August 6	—	34.0	47.5	13.5	1.6	3.8	3.7	1.5	Same parent
August 6	—	35.8	50.2	14.4	1.7	3.5	3.6	1.5	
October 10	—	46.0	64.0	18.0	2.2	3.8	3.5	1.8	Born about October 8
November 6*	—	52.0	74.0	22.0	2.3	3.7	3.8	2.0	Aborted
December 13	—	54.5	75.0	20.5	2.5	3.8	3.7	2.0	Born about October 15
July 19	—	69.0	90.0	21.0	2.6	4.3	4.5	—	Immature
June 24	—	74.5	104.0	29.5	2.6	4.1	4.1	2.1	Immature
August 1	—	82.5	116.5	34.0	2.7	4.3	4.5	2.4	Immature
August 1	—	90.0	98.0	x	2.6	4.4	4.5	2.4	Immature
March 23	—	98.4	141.2	42.8	3.0	4.7	5.6	3.1	Immature
August 7	m	111.9	141.5	x	3.3	5.2	6.2	3.3	Subadult
March 23	m	124.2	183.5	59.3	3.6	6.0	6.7	3.5	Adult
March 23	m	135.8	182.2	x	3.8	6.4	6.8	3.8	Adult
March 23	m	145.8	192.8	x	3.9	6.3	7.4	4.1	Adult
March 23	f	156.0	172.2	x	4.1	6.6	7.4	4.0	Adult
August 6	f	176.0	228.0	x	3.9	6.5	7.1	3.8	Adult

sues. They were, in the coiled position, 4.5 by 3.8 mm. At this early stage the eye was black and the snout was short.

An embryo with a snout-vent length of 12.0 mm. had a tail length of 6.0 mm. The eyes were black and the pupil white. The snout was short and the cranial bulge high. The supraoccipital bones appeared as two round white dots. The vent region was swollen, as the copulatory anlagen were just beginning to protrude from the cloaca (Coe & Kunkel 1906: 372, 383). The embryo was beginning to elongate, only the posterior half of the body being tightly coiled. The two embryos in this stage were killed on July 3, 1931.

The embryo of 23 mm. snout-vent length had a tail 8 mm. long. The body was folded once and the tail was coiled. The pineal organ as well as the eye were pigmented. The heart appeared to be pigmented also (perhaps from coagulated blood). The copulatory anlagen were fully protruded from the corners of the vent. They remain in this position until shortly before birth, when they are withdrawn into the cloaca (Coe & Kunkel 1906: 372, 383). The snout had elongated and the cranial flexure was less noticeable. The snout did not yet overhang the lower jaw.

One embryo of this stage was cleared in KOH and stained with alizarine red. The supraoccipital bones were the only well ossified structures. Narrow lateral margins of the parietals and frontal were beginning to ossify. The maxillary, articular and dentary were also slightly ossified. The pterygoid was more heavily ossified, but not as much as were the supraoccipitals. The seven anterior neural arches were slightly ossified.

The embryo of 29 mm. snout-vent length had a tail 11 mm. long. The body was folded twice and the tail was straight. The advances over the 23 mm. embryo were two: the outlines of the body scales and head plates could be seen, and the frontal bone was forming and had increased the interorbital width. The tip of the tail appeared to be lengthening through the activity of a terminal growth bud.

By the time the embryo has reached a snout-vent length of 35 mm., the outlines of the scales and head plates are clear. The scales are arranged in transverse and longitudinal rows and are slightly overlapping. The rostrum overhangs the lower jaw. The pineal organ is under the center of the interparietal plate. The nostrils are slightly elevated, giving the snout a square appearance. There is one lateral line on each side which fades posteriorly. The dorsal line is faint and also fades posteriorly. The copulatory anlagen still protrude.

Early in October, 1939, a young lizard was born which was 60.0 mm. in total length and weighed 0.275 grams. The head was long, narrow and pointed, with bulging eyes. The dorsal line was distinct on the silvery upper parts; the sides of the body were dark. The venter was flesh colored and the internal organs were clearly visible through the thin skin. When put in sand, it dug in readily, although slowly. It lived about ten days.

An individual of 46 mm. snout-vent length was born alive in October, 1939. The total length was 64 mm. and it weighed 0.32 grams. It lived about two days. The dorsal stripe was present, being black and silver. There were four fine dark stripes on the margins of the scales on each side of the mid-dorsal stripe. Lateral to this was a dorsolateral

stripe two and one-half scale rows wide. The centers of the scales of the dorsal rows between the wide lateral stripes were pinkish silver. Ventrally from this stripe to the midventral line the skin and scales were coral pink (Ridgway 1912: XIII-5'-d). The ventral side of the tail was like the dorsal side—pinkish silver with narrow diffuse longitudinal lines between the scale rows. The head was silvery, darkening anteriorly on the sides and below. The throat was silver with dark longitudinal lines between the scale rows. The internal organs showed through the thin-skinned venter, altering the color locally. The interparietal plate was completely fused with the frontoparietal.

An individual of 52 mm. snout-vent length was born dead in the embryonic membranes. The body was folded once, and the 22 mm. tail was straight. The lizard appeared to be ready to shed, and the body skin was easily removed with the aid of a needle. This condition appeared to be normal, except that the head was not ready to shed and the scales under the shed skin were dull instead of shiny. By all indications, if this lizard had been alive, it would have shed soon after birth.

A lizard of 54.5 mm. snout-vent length was born alive in October and lived until mid-December. Its total length was 75.0 mm. The weight in October was 0.525 grams, and in December 0.42 grams. During the two months of its life this lizard was very active.

#### GROWTH

At birth, I found the lizards to be approximately 50 mm. from snout to vent (65-75 mm. total length). Coe & Kunkel (1906: 351) state that "at the time of birth the young lizards are usually 70 to 80 mm. in length."

The rate of growth varies with the individual and the environment. Judging from field records and gonad development, the lizards are about 80 to 90 mm. from snout to vent at the end of their first year. Lizards two years old are from 80 to 120 mm. from snout to vent, and some are sexually developed. Further age determination should not be attempted; however, it may be safe to assume that the females are at least two years old, probably three, before they breed. The gonads of subadult lizards are approximately 2 mm. in length.

Lizards of snout-vent lengths from 120 to 135 mm. show little seasonal change in the gonads which are usually 3 to 5 mm. long. All males over 135 mm. that were examined showed marked seasonal variation in the length of the testis. Individuals of the same size have testes averaging one millimeter longer in the summer (breeding season) than in the spring (3.9 to 6.8 for summer and 3.0 to 5.7 for spring). One testis of a lizard killed in summer was 18 mm. long. The lengths of ovaries were much more variable than those of the testes.

The smallest female containing embryos was 126 mm. from snout to vent. The two developing eggs were 26.4 and 22.4 mm. long, respectively. The large-

est female was 176 mm. from snout to vent whereas the largest male was 154 mm.

Age groups based on field records may roughly be designated by body size.

	Snout-vent length
Immature—Young of the year, not sexually developed	46 to 82 mm.
Two years old, not sexually developed (probably females)	82 to 110
Subadult—Two years old, sexually developed, but probably non-breeding	82 to 120
Adult—Breeding, probably at least three years old	120 to 160
Old adults	160 and up

The growth of five black limbless lizards was followed in the laboratory at Berkeley (Table 2). The conditions in the laboratory were not natural, nor was the food eaten by the lizards. Because of the more uniform temperature than in the wild (16° to 25° C. at all times) and the vitamins added to the food, these growths must not be used in age determinations. However, a broad generalization can be drawn: the rate of increase in body size is inversely proportional to actual body size.

TABLE 2. Growth of *Anniella* in the laboratory at Berkeley, California; measured in millimeters.

Number of months in captivity	SV before	SV after	Increase	Per cent increase per year
<i>A. p. pulchra</i>				
7.....	66.0	98.0	32.0	83.0
4.....	71.0	94.0	23.0	97.1
7.....	87.0	96.0	9.0	17.7
8.....	98.0	119.0	21.0	32.1
8.....	103.0	138.0	35.0	50.9
7.....	113.5	116.5	3.0	4.3
8.....	116.5	121.0	4.5	5.8
6.....	120.5	123.0	2.5	4.1
<i>A. p. nigra</i>				
6.....	77.0	81.0	4.0	10.3
9.....	109.0	139.0	30.0	36.8
9.....	129.5	134.0	4.5	4.4
9.....	135.0	138.0	3.0	—
9.....	154.0	154.0	—	—

#### LIFE CYCLE OF *ANNIELLA PULCHRA PULCHRA*

The life cycle of *A. p. pulchra* is similar to that of *A. p. nigra*, but it is probably more variable because of the more diverse climatic conditions under which *pulchra* occurs. One embryo (67.0 mm. SV) was taken from a female in Kern County on September 15, 1931. This embryo was folded once and appeared fully developed. Two embryos were taken from a female in Los Angeles County on November 11, 1908, which were not as well developed (42.0 and 43.0 mm. SV) as the specimen from Kern County. Klauber (1932: 5) reports that "a specimen collected August 31, 1926 (body length 131 mm.), contained two apparently fully developed embryos 69 and 66



mm. long. They are light colored with normal longitudinal lines clearly defined. They are folded three times in the egg membrane." The aforementioned embryos, 42.0 and 43.0 in snout-vent length, were 60.0 and 68.5 mm. total length respectively, and were probably in approximately the same stage of development as the two embryos reported by Klauber in August.

Klauber (1939: 96) reports another embryo taken from a female which "was 142 mm. [total length], body length 109 mm., tail incomplete." The total length of the embryo was 97 mm., whereas the body length was 63 mm. This female was killed on November 10, 1938, at Pacific Beach, San Diego County. These four records of embryos indicate different breeding seasons for lizards in Los Angeles, San Diego, and Kern counties.

The smallest female containing embryos known to me is 109 mm. SV. The largest male is 185 mm. SV, whereas the largest female is 155 mm.

The growth of eight *A. p. pulchra* was closely followed in the laboratory at Berkeley (Table 2). As stated before, these figures cannot be used to determine age, but they do show general trends. They also show that the rate of increase of size of *pulchra* is greater than that of *nigra*. In other words, *pulchra* matures younger than does *nigra*. This has already been indicated by the size of the smallest breeding female of the two subspecies (*pulchra*, 109 mm. SV; *nigra*, 126 mm. SV).

#### SHEDDING OF SKIN

Ecdysis in the limbless lizard is preceded by a characteristic color change. As the highly polished cornified surface layers of skin break away from the deeper layers, a change is produced. As soon as the loosening is complete and the newly formed outer surface of the skin becomes polished, the original coloration returns.

The first indication of shedding in an adult *A. p. nigra* is the change of color from black to light blue (Ridgway 1912; deep green-blue gray XLVIII-45' - b) which takes one or two days. The light blue phase remains for from five to eight days. The return to normal coloration progresses from the tail toward the head, which is the last to become dark again. This darkening is accomplished in from three to five days. The lizard then appears normal, but dull, for a day or two until the skin begins breaking away in fragments. The neck area usually loosens first, and the lizard slips out of the skin leaving it in tightly pleated cylindrical pieces. There is no muscular activity correlated with shedding as is employed by snakes. The head plates are usually the last to shed.

The rapidity of shedding is dependent on the amount of moisture in the substratum. If the sand is dry, the cast skin may adhere to the new skin for some time and the head may not shed at all. The old dry skin on the head makes feeding and the use of the eyes difficult. The lizards become sluggish and

apparently sometimes starve to death. If the sand is damp, however, the cast skin absorbs moisture and sloughs off in one to two days. The complete ecdysis may be accomplished in from nine to twenty days. Under field conditions it is probably completed in about ten days.

The frequency of shedding varies with the activity of the individual lizard. Under laboratory conditions lizards shed every three to five weeks, from February to November. Activity was less during the winter months and some lizards did not shed at this time.

The color change prior to casting the skin is less noticeable in the more silvery individuals, and in *A. p. pulchra* it can only be seen along the longitudinal lines.

#### REGENERATION OF TAIL

The incidence of tail regeneration in the limbless lizard is high, being 59 per cent of the 161 *nigra* and 69 per cent of the 79 *pulchra* examined by me. The regrown portion is a short black cone and is the same in the two subspecies.

The regrowth of the tail of a lizard in the laboratory took nearly a year. About one week after the break, the stub was rounded and covered with pink skin. Six months after the break the regrown tip was 3.0 mm. long. The pink skin covered only the apex and was 1.0 mm. in diameter. The rest of the cone was covered with small black scales. The pigment was first deposited on the dorsal half of the new tail. After eleven months the regeneration was complete, the new tail being 4.1 mm. long and covered with black scales. The margin between the caudal scales and regenerated scales was marked only by the reduction in size of the latter.

#### ENEMIES

Because the limbless lizard is subterranean, it has few enemies. Listed below are those animals which are known to have attacked or devoured either *A. p. pulchra* or *A. p. nigra*.

Man (*Homo sapiens*)  
House cat (*Felis domesticus*)  
White-footed mouse (*Peromyscus maniculatus*)  
Loggerhead shrike (*Lanius ludovicianus*) (Fisher 1901: 48)  
Boyle king snake (*Lampropeltis getulus boylii*)

There are, in addition to the above, several animals which inhabit the same terrain as *Anniella* which might be potential enemies. These are:

Dog (*Canis domesticus*)  
Norway rat (*Rattus norvegicus*)  
Ground squirrel (*Citellus beecheyi*)  
Meadow mouse (*Microtus californicus*)  
Pocket gopher (*Thomomys bottae*)  
Mole (*Scapanus latimanus*)  
Crow (*Corvus brachyrhynchos*)  
Alligator lizard (*Gerrhonotus coeruleus* and *Gerrhonotus multicarinatus*)  
Gopher snake (*Pituophis catenifer*)  
Racer (*Coluber* sp.)

The high percentage of regenerated tails suggests that some formidable enemy is thwarted by the autotomy. This might be such forms as mice or moles. Hot sand or direct sunlight may be a factor in injuring the tails of the lizards. It was found that when a lizard digs into the sand, the end of the tail is often left exposed. It was also noted that the sensory nervous supply to the tail is much less than to the rest of the body (see below). By leaving the tip of the tail exposed the lizard leaves itself open to attack from any number of roving predators. In addition, if the exposed tail should be in the direct rays of the sun, the temperature may be raised above the lethal point (40° C.) and the tissue killed. This occurred in a laboratory experiment and the lizard regrew a black tip on the tail where the injured tissue had sloughed off.

#### DEFENSE

When a lizard bites, the strike is slow and deliberate. This is often not completed, being apparently a bluff. However, when a good grip is attained, the lizard bites hard a few times then releases its hold. Usually the bite is not painful but the pinch is strong and might be harmful to soft tissue.

When the lizards were crowded and without cover, they often bit each other, sometimes drawing blood. When bitten on the tail, there is no excitement, but when bitten on the body they writhed as if in great pain. The attacker usually held on a few seconds and was thrown about by the contortions of the victim.

#### PARASITES

Two internal parasites but no external ones were taken.

A nematode is often found in the colon of both *A. p. pulchra* and *A. p. nigra*. These round worms are white and about five millimeters in length. There may be from two to eight worms in one lizard.

In his recent paper on oxyurid nematods, Walton (1941: 16) states that these worms "undoubtedly belong to the genus *Thelandros*, thus increasing the range of the genus to include the southwestern coastal area of the United States." Previous to the discovery of these worms in the limbless lizard, members of this genus had been reported only from African, South American, Australian and Asiatic reptilian hosts. Walton states further: "no attempt is made to give a species designation to this *Thelandros* form [from *Anniella*] since the material consisted entirely of female specimens with the exception of enough fragments of a male to enable the definite generic identification to be substantiated."

A cestode has been taken from two *pulchra-nigra* intergrades at the mouth of the Salinas River and from one *nigra* from Pacific Grove, Monterey County. Dr. Stunkard writes that it is an anoplocephaline tapeworm of the genus *Oochoristia*, but that specific identification is not possible with the available material. One of the infected lizards had five tapeworms in its intestine; the scolices were just below the stom-

ach. The presence of these parasites had no visible effect upon the hosts.

### STRUCTURES AND ACTIVITIES RELATED TO FOSSORIAL LIFE

#### LIMBS

Externally there are no traces of either pelvic or pectoral limbs in *Anniella*. Internal vestiges remain, however. Camp (1923: 468, Figs. 70-72) illustrates the cartilaginous clavicle which is buried in the musculature of the shoulder region. The rest of the pectoral elements are entirely lacking. The pelvic girdle is also reduced. Cope (1900: 673) states: "the ilium is represented by a small and short rod-like bone, which is attached to the extremity of the diapophysis of a single vertebra. The proximal extremity is directed backward for a short distance posterior to the point of suspension, as in *Anelytropis*. According to Baur, there is a rudimentary ischium and pubis, 'which are united proximally.' No trace of posterior limb."

#### LOCOMOTION

In the absence of limbs, locomotion is achieved by undulatory body movements. There are no scutes as in snakes, or annuli as in amphibiaenids, nor are there setae as in earthworms to aid in progression. The body surface is covered with smooth highly polished imbricated scales which reduce friction with the substratum.

The basic locomotor pattern is a lateral sigmoid undulation of the body, which is started by the head. If a fixed object is available the lizard will "push" itself along, the point of contact being constantly shifted posteriorly. On a smooth surface, such as glass, progression is practically impossible; the lizard twists and bends ineffectually. On smooth fine sand, however, the lateral swing of the body raises small ridges in the sand (Fig. 4). The lizard pushes against these ridges and progresses forward.

When a lizard is put onto a smooth surface of dry sand, the first movement is usually an elevation of the neck with a subsequent forcing of the snout down into the sand. At the same time the body pushes against the substrate, raising little ridges for traction, and the head is moved back and forth quickly as if parting the sand (Fig. 2). When any cuneiform object is pressed into sand, it slides in among the grains easily. If moved from side to side,



FIG. 2. *Anniella pulchra pulchra* digging in. Note indication of the lateral movement of the head.

much less pressure is required to force it into the substrate. The lateral movement of the cuneiform head of the lizard is slight, but it is repeated rapidly, thus literally packing the sand on each side. The lizard moves forward at the same time by the force of the body pressing against the ground. As soon as the head is under the surface it turns to one side, starting a sigmoid curve. After approximately one inch of the body is in the burrow the force is all exerted on the first undulation underground; the rest of the body often swings around with only the tail marking the sand.

Sometimes a vertical movement of the head replaces the lateral swing. This is only when the compactness of the sand hinders further lateral compression. If a lizard is several inches below the surface in a jar and approaches the glass, the head is moved up and down, compacting the sand vertically because the lateral compression is impossible on one side. However, when a lizard was put into a narrow glass cage slightly wider than the lizard itself, it turned on its side and used the lateral motion of the head to part the sand as it dug. In this way it was also able to start a curve under the surface in the same manner as if the cage was horizontal.

Subsurface progression is accomplished in the same manner as surface progression except that the head must cleave the sand to allow the body to pass through. Traction is much greater below the surface, as the entire body is used to exert force on the substratum. Movements underground are generally slower than on the surface. In digging in, an eight-inch lizard disappeared under the sand in six seconds.

Movements are easier for the lizards when within one inch of the surface. At this depth the sand is not only compacted laterally as the lizard moves through it, but is also raised into a ridge on the surface. A groove is left in the surface of the sand after the lizard has passed (Fig. 3). These surface grooves may be used as field "signs" indicating the presence of the lizards. However, beetles (*Coelus ciliatus*) form similar grooves in great numbers. The beetle grooves differ from lizard grooves in being narrower (about  $\frac{1}{4}$ -inch across) and by having sharp

angles. The grooves made by lizards are usually at least one-half inch across and follow smooth curves.

In damp sand, which is characteristic of the deeper layers in sand dunes, the tunnels do not collapse. One such tunnel was followed for about sixteen inches near the trunk of a large lupine bush at Carmel. It paralleled the surface at a depth of 1 inch.

In the laboratory the deeper tunnels were observed against the glass sides of the cages. Lizards were frequently seen moving both forward and backward; there were many periods of inactivity. The deep tunnels were changed constantly as were the entrances on the surface.

Since the limbless lizard usually occurs under bushes or leafy litter on the surface of the ground, these grooves and burrows are not often encountered in the field. However, where trash such as boards, logs and similar cover is present, the burrows are often exposed by moving this cover. A glass plate was laid firmly on the sand in the cages and the lizards on coming to the surface made burrows under the plate. These burrows were changed frequently, as were those at deeper levels.

#### MIDVENTRAL GROOVE

On the ventral surface of live *Anniella* there is a longitudinal groove which extends from just behind the throat to the vent. The presence of this groove produces a double-keeled ventral surface. Mosauer discusses these adaptations in sand-dwelling forms such as *Uma notata*, *Chalcides sepoides*, and *Sonora occipitalis*. He (1932: 76) states that "it seems reasonable to assume that the crescentic cross section of the body of the subarenaceous forms has a mechanical significance in burrowing, functioning as a double keel and thus preventing slippage in the horizontal undulations of the body."



FIG. 5. Outline of cross-section of body of limbless lizard, x  $1\frac{1}{2}$ .

#### CANTHUS ROSTRALIS

The snout projects over the lower jaw and is formed by the rostral and upper labial plates. This forms a cuneiform wedge with the lower jaw "counter-sunk" on the ventral surface. The rostral and upper labial plates are folded in the center, forming a smooth pointed edge (Mosauer 1932: 75-76; 1935: 17). *Anniella geronimensis* presents the sharpest canthus rostralis of any member of the genus.

#### EYES

The eyes of *Anniella* are small and deep set. They are functional and are covered by a lower lid bearing three scales. These scales are shed with the head plates. Early workers were in disagreement

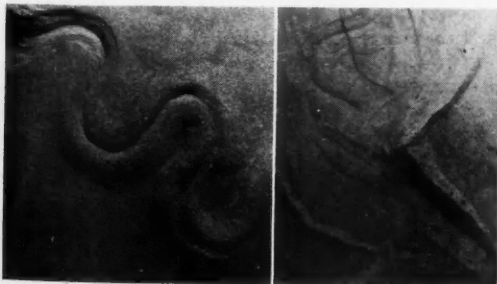


FIG. 3. Groove made by subsurface progression of a limbless lizard. The lizard is in the lower right part of the groove.

FIG. 4. Ridges made by surface progression of a limbless lizard.

about the eyesight of these lizards; the most extreme view was that of Ditmars (1907: 168): "The eyes are covered with translucent skin and are useless."

Anniella appears to be near-sighted. In the laboratory a lizard in a burrow under a glass plate (see p. 279) followed a small beetle larva which was on top of the glass. The larva moved above the burrow for three inches. The lizard followed closely within the burrow and repeatedly struck at the larva. The larva was about one-half inch from the lizard's eye. The larva then moved away from the burrow and when the lizard could no longer see it, the chase was given up.

The sudden approach of a large object, such as a man approaching the cage, usually caused the lizards to withdraw from the surface of the sand or from under the glass plate. Slow movements at a distance of two feet or more produced no reaction.

The eyes are closed when the lizards move in dry, unconsolidated sand. In open burrows in damp sand, however, they are open.

#### EARS

There is no external ear opening. The lizards have keen perception of mechanical disturbances close to them. In feeding a lizard which had come to the surface with just the head above the sand, a beetle larva often bumped the snout of the lizard. The lizard would immediately withdraw and come to the surface ahead of where the larva was crawling and catch it.

On several occasions lizards were observed with the head on the surface but with the otic region below the sand. They often remained in this position for ten minutes or more. The nostrils were above the sand and the eyes were open. The lizards gave the appearance of being on guard or "still hunting."

#### NARES

The external nares are situated on the crest of a slight elevation in the nasal plate. They are not closed or protected by overhanging scales. However, the nasal plate extends into the nares, forming a tube, which is connected with an intranasal process, the surface of which is shed with the nasal plate.

Eddy (1906: 638) in discussing the brain of *A. pulchra* mentions "the large olfactory lobes closely applied to the forebrain . . . the small otic lobes and the very small cerebellum." Morphologically then, the olfactory organs seemingly are well developed.

The tongue as well as the nasal passages is probably associated with olfactory sense. The tongue is often "licked" out as if testing the air. In the laboratory in winter the lizards would extend the head vertically about an inch out of the sand and lick the air a few times with the tongue, while apparently looking around. After about ten to thirty seconds they would retreat beneath the sand. Usually they came from deep in the sand to make this observation.

#### SENSE OF TOUCH

A positive thigmotropism is definitely correlated with the fossorial habits of these lizards. They require contact with some substance on their backs and sides. When just enough sand to cover them was provided, the lizards moved only occasionally. However, when no sand or cover of any sort was present, the lizards were erratic and uneasing in their movements. They did come out of the sand but this was usually under the cover of the leafy layer on the surface or under the glass plate. It was noticed several times that when the laboratory animals came out of the sand with no cover present they would not remain on the surface but dug in almost immediately. When given a choice between cover and no cover, they invariably sought the cover. When placed on the surface of sand, they always dug in.

#### VERTEBRAE

The number of rib-bearing vertebrae is large due to the elongation of the body and the need for additional support for the posterior trunk region. There are seventy-three rib-bearing vertebrae in *Anniella* (Cope 1900: 673).

#### LUNGS

The right lung is elongated and well developed. The left lung is small or rudimentary, although it remains functional (Coe & Kunkel 1906: 360, Fig. 8).

#### REPRODUCTIVE ORGANS

Both testes are present, the right testis lying anterior to the left. The ducts are normal. Both ovaries are present; the right one is anterior to the left. The left oviduct is either absent or vestigial (Coe & Kunkel 1906: 374, pl. XLIII). The right oviduct is normal and receives ova from both ovaries.

#### ECOLOGICAL RELATIONS

The range of *Anniella* lies in the western part of central and southern California and in northwestern Lower California. This region is diverse in both topography and climate. The major units are: the coast region, the San Joaquin Valley, the foothills of the Sierra Nevada, the valleys of the interior of southern California, the edge of the Colorado Desert, and the Sierra San Pedro Martir.

*Anniella pulchra nigra* occupies a region of uniform climate, the Transition Life-zone, on the coast from Santa Cruz County (possible San Francisco County) south to San Luis Obispo County where it intergrades with *A. p. pulchra*. The latter occurs in a similar climate on the coast, and also in wetter, drier, hotter and cooler climates in the San Joaquin Valley, in the various mountain ranges, and at the edges of the desert. It occurs in Lower and Upper Sonoran, Transition and possibly Canadian life-zones.

#### TERRAIN

Limbless lizards have been taken from many types of terrain. A few of the typical regions are discussed below.



Coastal sand dunes.—The sand dunes at Carmel, Monterey County, are on a terrace seventy-five feet above the beach. The sand is white and fine grained (84.6 per cent of the grains are from 0.2 to 0.5 mm. in diameter). The vegetation is sparse and is dominated by large lupines (*Lupinus arboreus*) and mock heather (*Ericameria*). Cypress trees form vegetation "islands" in the draws (Fig. 7). The black limbless lizards are found in the sand and leafy litter under the edges of the bushes.

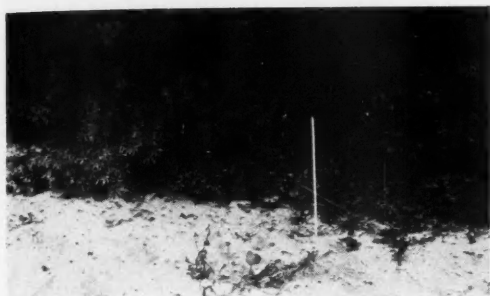


FIG. 6. Habitat of the black limbless lizard at Carmel. The thermometer marks the zone where the lizards "bask" in the warm sand. Note the leafy litter beneath the lupine bush (*Lupinus arboreus*).

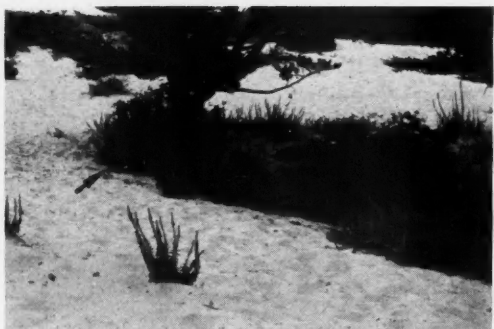


FIG. 7. A cypress group in the Carmel sand dunes. The thermometer, located by the arrow, is shown in Figure 6.

The sand dunes along Monterey Bay form long narrow tracts. In many localities they form spits between the bay and tidal sloughs. The sand is coarser here than at Carmel. The vegetation is generally sparse toward the sea and heavier toward the land. The sparse vegetation is dominated by sand verbena and low lupines. To the leeward the large yellow lupines and mock heather are dominant. The lizards are more common near the larger vegetation.

At Watsonville the dune areas are divided into grass associations (*Ammophila arenaria*) and lupine associations (*Lupinus arboreus*) (Fig. 9). The lizard taken here was in the lupine association.

Sand hills.—The sand hills east of Antioch, Contra Costa County, form the south bank of the San Joaquin River. The sand is loose and fine grained (53

per cent of the grains are 0.2 to 0.5 mm. in diameter and 36 per cent are from 0.1 to 0.2 mm. in diameter). The dominant vegetation is annual grasses, herbs and live oak trees. Lupines (*Lupinus arboreus*) are found near the river. The silvery limbless lizard occurs in this region near the oaks, usually under boards, logs or other refuse.

Western San Joaquin Valley.—Lyle Christie found several specimens of *A. p. pulchra* on the Lillis Ranch, "30 miles southwest of Mendota, Fresno County." In the spring of 1936 he was building a road through a diatomaceous formation known as the Kreyenhagen shale when he found some silvery limbless lizards at a depth of approximately two feet. He writes that this "shale is always dry, on a slope with a south exposure, and it is only in the very wettest of years that even grass grows on it." A year or so later he dug out several more lizards in approximately the same place. In February, 1938, another specimen was taken under a "fairly large rock" in a "cool damp place in the shade of an old cottonwood tree." The sites of collection in 1936, 1937 and 1938 were all within three hundred yards. In January, 1940, another lizard was dug up. This site "was about two miles distant from the first previous localities, up the canyon, the difference in elevation being about three hundred feet."



FIG. 8. Habitat of the black limbless lizard on the second islet off Point Pinos. Note the shells in the earth at the base of the *Eriogonum* bush.



FIG. 9. The lee of the sand dunes 4 miles west of Watsonville, showing the change from the grass association (*Ammophila arenaria*) on the right (seaward) to the lupine association (*Lupinus arboreus*) on the left.

Mr. Christie summarizes his observations as follows: "In all cases the lizards were found either on the banks of the creek, or the very edge of the bank, but that may have been a coincidence because that happened to be where we were working most frequently. In no case was there any brush, and only in one place does much grass grow. At the time we found the lizards it was always cool, but this again may be because in hot weather we do very little of such work as to uncover them."

The Lillis Ranch is situated on Cantua Creek, which drains the eastern slope of the Coast Ranges and flows into the San Joaquin Valley. It rises in the Upper Sonoran Life-zone and flows from the hills into the Lower Sonoran of the valley. Judging from Mr. Christie's reference to the three-hundred-foot rise in the stream in two miles, the sites where *Anniella* was taken are probably in the lower edge of the Upper Sonoran Life-zone.

Interior valleys of southern California.—The silvery limbless lizard is reported by Hilton to be "common, but not abundant" near Claremont in eastern Los Angeles County. The lizards are found in the upper portions of the alluvial fans. One collection site which I examined was in the "wash" area adjacent to the present stream bed of Thompson Creek, which ultimately drains into the Santa Ana River. This creek flows only during heavy storms. The vegetation is dominated by black and white sage (*Salvia*) and chamise (*Adenostoma*). Several species of cactus (*Opuntia*) and buckwheat (*Eriogonum*) are common. The vegetation is dense, chaparral-like, with open spaces between the plants forming narrow paths. The earth is hard, except in local areas under the bushes where leafy refuse has accumulated. The soil of the region is generally fine grained, with a high percentage of stones and boulders.

#### EFFECT OF TOPOGRAPHY AND COVER

Hall & Grinnell (1919: 39) point out the effect of slope exposure, air currents and succession of vegetation on the local distribution of life-zones. These factors apply in the same way when considering the microrelief as when considering the gross topography. The south-facing slopes of sand dunes are warmer and drier than the north-facing slopes; the lee side of a coastal dune chain is warmer than the windward side. The moving dunes with sparse low plants undergo greater extremes in temperature, moisture, and exposure to the wind than stable dunes with higher shrubs and trees.

The presence of vegetation alters the local conditions in sand dunes by resisting wind erosion, adding humus to the sand, holding the moisture near the surface of the sand, and preventing extreme temperatures. The flora also makes possible the existence of a large insect fauna, which lives mainly in the leafy litter that accumulates under the plants.

The distribution of vegetation in coastal sand dunes is determined by the exposure, there being generally more plants on the north-facing than on the south-



FIG. 10. Deciduous oak-grass association in Carmel Valley (12 miles east of Carmel) where W. K. Fisher found silvery limbless lizards.

facing slopes. The larger plants are usually on the lee of the dunes protected from cold winds and sand abrasion. To the windward the low more resistant plants are dominant, all vegetation decreasing toward the beach.

The interaction of microrelief and vegetation affects the moisture and temperature of localized areas. For example, under a large lupine bush in midwinter the sand was cold and wet. On one side of the bush, however, there was a relatively restricted zone of drier, warmer sand. This drier area was protected from the micro-wind currents, as the bush had collected most of the rain on its windward side.

The sand temperature was notably affected late one morning in September. The sun had come from behind heavy fog only about ten minutes before the temperatures were taken at the sunny side of a bush on a gentle south slope (Fig. 11). The difference between the surface temperature under the bush (24.8° C.) and adjacent to it (40.0° C.) shows the effect of the bush in preventing extremes of sand temperature. Adjacent to the bush the difference between the surface temperature (40.0° C.) and the temperature one inch deep (25.5° C.) was probably due to the warmth of the direct sunlight. However, the difference between the one-inch temperature (25.5° C.) and the six-inch temperature (23.2° C.) was due to the warmth accumulated during the overcast morning. Under the bush two inches below the surface the sand was 2.5° C. cooler than six inches deep at the periphery of the bush. These temperatures had probably not been altered by the warmth of the sun that morning. This shows cumulative effect of the bush on the ground temperatures. The average temperature beneath the bush was lower than the average temperature adjacent to it (see beyond).

#### TEMPERATURE

The daily variation in temperature depends on the weather and the season. Fog, clouds, rain and bright sun all influence the temperature of the soil. The depth to which the temperature changes daily depends on the degree of obstruction of the sun's rays,

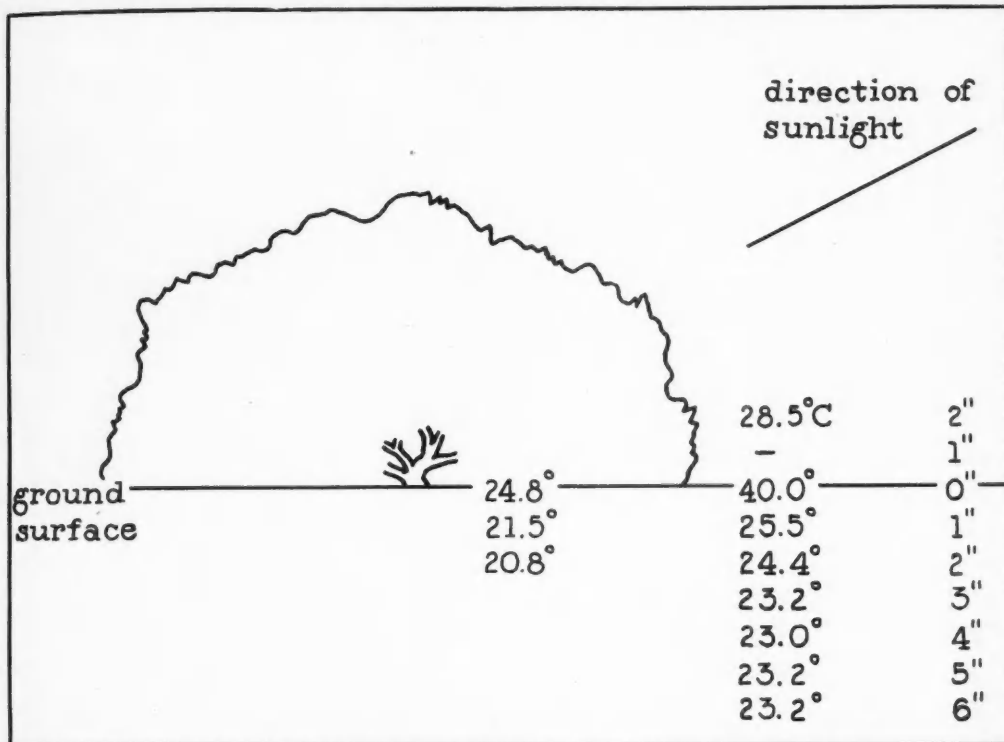


FIG. 11. The effect of a bush on the temperature of the ground.

the amount of moisture in the surface ground and in the air and the direction of the wind. On a windy overcast day the surface of the ground warms but slightly when compared with a bright calm sunny day.

Figure 12 shows graphically the temperature changes during an average day from the surface of the ground to a depth of twenty-four inches. The gradients figured here were determined in open sand dunes adjacent to vegetation but not under it. For this average clear day let us assume that at dawn the temperature at the surface of the ground is 10° C. and the temperature ten to twenty-four inches deep is 20° C. During the morning the surface warms first and the gradient begins to rise. As the heat penetrates, the gradient becomes smoother and at the middle of the day it has become inverted. During the afternoon the gradient declines slowly; after sundown it falls more rapidly and by the next dawn has returned to its original form. On an overcast, rainy or windy day the gradient follows the same pattern to varying degrees of completion.

Since the daily modifications of the gradient are not all the same, the temperature at a depth of over ten inches rises and falls slowly. If the midday temperatures are repeatedly high, the deep temperature will increase; however, if the heat at the surface is diminished through cloudiness the temperature of the deeper zones will decrease. The temperature

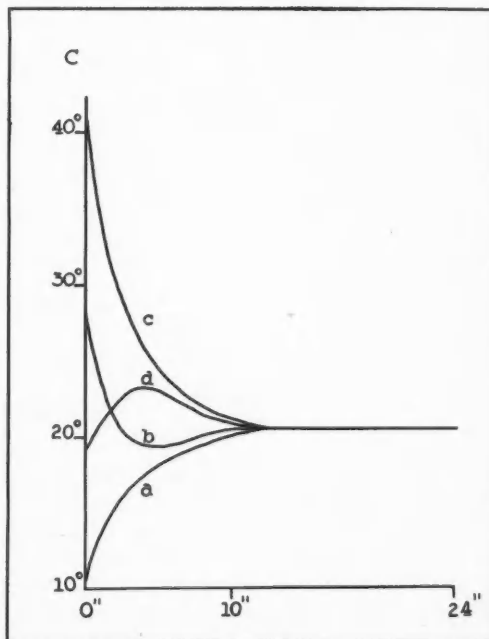


FIG. 12. \* Temperature gradients in sand during an average clear day. a, dawn; b, midmorning; c, midday; d, late afternoon.

from ten to twenty-four inches, then, is a result of many daily extremes, and may be termed the average or mean temperature for that spot at that time. At Carmel this deep temperature varied with the season (Table 3).

TABLE 3. Sand temperatures at a depth of over ten inches, showing seasonal change; taken in the sand dunes at Carmel, California.

	Temperature	Depth
September 23, 1939.....	23°C.	8"
November 25, 1939.....	16-17°C.	15-24"
January 19, 1940.....	12-13°C.	15-24"
March 21, 1940.....	16°C.	15-24"
May 23, 1940.....	17-18°C.	15-24"
September 11, 1940.....	23.5°C.	6"

The daily variation of temperature appears to control directly the activity of the lizards. In the morning they are often found basking in the warm sand near the surface while in the afternoon and evening they are active in the leafy litter beneath the bushes. It is during the decline of the temperature gradient that the lizards feed.

Under laboratory conditions the temperature varied in winter from 17° to 22° C. and in summer from 20° to 26° C. The lizards were more active during the afternoon and evening (roughly from twelve noon to nine p.m.) than at any other time.

The lowest temperature at which lizards were active in the field was 13.5° C. (*A. p. nigra*). On the occasion of this record the lizard was moving through wet leafy litter beneath a bush at ten-thirty p.m. in February. The lowest temperatures at which lizards were taken in the field were 10.5° C. (*pulchra*) and 13.2° C. (*nigra*) (Table 4).

TABLE 4. Temperatures at field collection sites (degrees Centigrade).

	<i>A. p. pulchra</i>				<i>A. p. nigra</i>			
	No. Coll.	Temperature °C.			No. Coll.	Temperature °C.		
		Min.	Max.	Av.		Min.	Max.	Av.
February..	6	10.5	41.5	10.80	5	13.2	15.3	14.38
March....	12	14.0	27.8	18.10	29	14.2	24.8	18.20
April.....	2	22.3	22.3	22.30	—	—	—	—
May.....	—	—	—	—	61	15.5	31.2	20.90
June.....	1	22.0	22.0	22.00	—	—	—	—
September.	2	22.0	23.3	22.60	—	—	—	—

The low temperature threshold of activity of *A. p. pulchra* from Antioch and of *A. p. nigra* in the laboratory was found to be 13° C. The lizards endured a temperature of 4° C. for twenty-four hours with apparently no ill effects.

The highest temperatures at which lizards were taken was 31.2° C. (*nigra*) and 27.8° C. (*pulchra*). The high temperature tolerances determined in the laboratory is 40° C. Temperatures above 40° C. are lethal.

The optimum temperatures of activity are probably from 15° to 25° C. The monthly averages given in Table 4 fall mostly within this range. Not all of the lizards tabulated were known to be active at the time of collection. Some were basking in the warm sand.

#### MOISTURE

The limbless lizards are found in regions of well-drained porous soil. They occur locally in situations where they can move from dry to damp soil. That moisture is essential to their activities has been pointed out in the discussion of shedding. Table 5 shows the moisture content at sites where lizards were collected.

TABLE 5. Moisture at field collection sites, by percentage of total weight of the raw soil sample.

	<i>A. p. pulchra</i>				<i>A. p. nigra</i>			
	No. Coll.	Moisture			No. Coll.	Moisture		
		Min.	Max.	Av.		Min.	Max.	Av.
February..	2	7.28	8.58	7.93	3	3.38	10.91	7.06
March....	5	2.71	9.54	7.27	27	1.82	25.82	16.46
April.....	2	6.84	6.84	6.84	—	—	—	—
May.....	—	—	—	—	33	1.09	16.60	9.06

TABLE 6. Organic matter present in the soil at field collection sites, by percentage of dry weight of some of the samples listed in Table 5.

	<i>A. p. pulchra</i>				<i>A. p. nigra</i>			
	No. Coll.	Organic Matter			No. Coll.	Organic Matter		
		Min.	Max.	Av.		Min.	Max.	Av.
February..	2	1.32	13.20	7.26	3	1.06	16.89	8.81
March....	5	2.29	3.79	3.16	21	10.05	25.90	16.26
April.....	2	2.79	2.79	2.79	—	—	—	—
May.....	—	—	—	—	7	3.08	26.45	14.15

The amount of moisture present in clean sand can be roughly designated by the following characters of the sand as a mass:

*dry*—will pour, will not press to cast; 0 to 1 per cent water.

*dry-damp*—will not pour, will press to cast, but breaks with release of pressure; 2 to 4 per cent water.

*damp*—will not pour, will press to cast, will not break with release of pressure but will break if touched; 5 to 7 per cent water.

*moist*—will not pour, will press to cast, will not break with release of pressure or if touched; 8 to 14 per cent water.

*saturated*—will not pour, will puddle if agitated; over 15 per cent water.

The highest soil moisture at which a lizard was found was 25.82 per cent of the total weight of the sample. This ground was highly organic (Table 7) and would be termed "damp" from the physical characters of the soil (see p. 286 for the effect of

organic matter on soil). At Carmel on February 24, 1940, another lizard was found moving through wet leafy refuse under a lupine bush in the rain.

TABLE 7. Soil moisture and organic matter content at collection sites of limbless lizards.

Month	Per cent moisture	Per cent organic matter
<i>A. p. pulchra</i>		
Contra Costa County		
February.....	8.58	1.36
	7.28	13.20
March.....	9.54	3.79
	7.52	2.45
	7.03	3.49
	2.71	2.29
April.....	6.84	2.79
<i>A. p. nigra</i>		
Monterey County		
February.....	10.91	16.89
	6.91	8.50
	3.48	1.06
March.....	25.82	25.75
	25.80	25.90
	24.66	24.25
	24.24	21.60
	22.99	20.90
	22.36	19.65
	21.98	13.65
	19.01	15.10
	17.76	13.85
	13.61	10.50
	13.36	16.40
	13.27	11.78
	13.14	10.05
	12.06	12.25
	9.72	14.95
	9.19	12.80
	8.91	11.78
April.....	—	—
May.....	11.80	26.45
	8.15	16.81
	7.40	12.40
	7.30	13.80
	7.00	15.60
	5.70	10.95
	1.09	3.08

The most moist sand which a lizard penetrated in the laboratory was a saturated mass rising but one inch above the level of adjacent water. One lizard remained in this situation for one month and apparently suffered no ill effects.

The limbless lizard was found to be able to swim for short distances, the lateral undulating body movements being made fast enough to propel the body forward. Usually, however, the lizards moved slowly as if moving through sand and they sank to the bottom. Movements under water were often aimless bends and twists accompanied by gaping of the jaws. The lizards drowned in about thirty minutes.

The lowest moisture recorded at a collection site was 1.09 per cent. This soil sample had only 3.08 per cent organic matter. The lowest moisture recorded in the field was 0.07 per cent. This sample was taken from the surface of a sand dune at Carmel at a temperature of 15.9° C. on January 19. The organic matter in surface Carmel dune-sand is approximately 0.1 per cent of the dry weight.

In the laboratory the lizards moved freely from dry sand (0.3 per cent water) to damp sand. The cages were set up with saturated sand (15 per cent water) one inch deep overlain with three inches of dry sand. Moisture diffused from the wet sand into the dry for about two inches. This diffusion zone varied from 1.3 to 1.8 per cent water. The lizards burrowed in the dry and diffusion zones, only entering the wet zone when it had dried partly.

The moisture present in sand dunes is shown in Table 8 in the form of profile readings taken at Carmel.

TABLE 8. Moisture content of the sand dunes at Carmel. All records were taken from samples at the south margins of lupine clumps, within fifty feet of each other; those for January and February were taken at the same spot.

Depth in inches	November 25, 1939	January 19, 1940	February 23, 1940
0.....	6.40	—	—
1.....	.25	—	—
6.....	1.09	.14	2.92
12.....	.85	6.35	4.64
14.....	5.55	—	—
18.....	—	5.52	7.49
24.....	—	2.58	19.70
30.....	—	—	16.30

mel. The great difference between the moisture at the surface and one inch below the surface on November 25 was the result of about 0.55 inches of rain which fell in the night of the 24th. The surface crust of wet sand was from ¼- to ½-inch thick the next day. The high moistures recorded on January 19 at a depth of 24 and 30 inches were from the heavy clay substratum which underlies the sand dunes. Under a large bush (*Ericameria*) on January 19, the moisture 36 inches deep in sand was 1.24 per cent.

#### LIGHT

The limbless lizard is not negatively phototropic as its subterranean, crepuscular and nocturnal habits might indicate. The lizards are most active under conditions of low illumination; however, the maintenance of burrows which were flooded with strong light (under glass plate) and frequent sojourns out of the sand in a brightly lighted room indicate the absence of a negative phototropism.

The visible rays of sunlight were found to penetrate sand from Carmel to a depth of five millimeters and Antioch sand to only three millimeters. The lizards usually are deeper than this in the sand or are under a board which also prevents light from reaching them. Nonvisible portions of the sunlight may penetrate deeper, and the pineal eye may be sensitive to these rays. The physiology of this organ in *Anniella* is still unknown (Coe & Kunkel 1906: 391).

#### SOILS

The limbless lizard is subarenaceous, usually inhabiting sand or sandy loam soil. There may be gravel, stones or boulders mixed with the finer soil.



On the islet off Point Pinos, Monterey County, the lizards have a choice of coarse gravelly sand or fine sandy humus soil of a shell mound. Most of them were found in the black humus soil which has a high percentage of broken shell fragments (Fig. 8).

The amount of organic matter present in the soil in thirty-four collection sites of the limbless lizard varies from practically none to 25 per cent. The presence of organic matter increases the amount of soil moisture without decreasing the airspace in the soil. Table 7 shows the moisture-organic matter relations at field stations.

Dune sand is low in organic matter (1 to 2 per cent) except under the bushes, where the leafy layer lies on the surface and mixes locally with the sand (approximately 8 per cent) for about an inch. The movements of the lizards and insects through the sand screen out the leafy chaff and pile it on the surface. The organic matter in dune sand plays a minor role in moisture retention but a major role in supporting the fauna of insects.

The depths at which the limbless lizards have been found are only approximate, as most of the depths were estimated rather than measured. "A couple of feet" is the most common depth referred to by persons who have dug them out while building roads or digging ditches. I have taken a lizard at a depth of eight inches and know of one reliable record of one being taken at a depth of twelve inches.

At Antioch twelve silvery lizards were found at depths of from one to three inches (average 2 inches). These were all under logs, boards or some other cover. Eleven others were found on the surface of the ground under logs or boards.

In the sand dunes of Monterey Bay and Monterey Peninsula, the black lizards were taken from the surface in the leafy litter beneath the bushes and down to a depth of eight inches (average 1.42 inches). They were also taken from the surface of the ground under boards.

The bottoms of the cages in the laboratory were the most common abode of the lizards, some being thirteen inches deep in loose sand.

The compactness of the soil and the moisture-airspace equilibrium determine the depth to which the lizards can penetrate. The compactness of the sand was recorded by a spring instrument shaped like the head of an *Anniella* which recorded the pressure exerted in grams. Steady pressure of the instrument required more force to penetrate the sand than pressure with a slight movement such as the lateral movement of the lizard's head. A pressure of 500 grams plus the lateral movement allowed the instrument to slowly penetrate a sand bank which could not be penetrated with a steady pressure of 2,000 grams.

At Carmel in January, the unconsolidated dry sand on the surface of the dunes offered less than 10 grams resistance. The damp sand two inches deep offered 200 to 400 grams resistance whereas the resistance of the sand over five inches deep was more than 2,000 grams. The greatest resistance was offered

at a depth of about twenty inches; below this the resistance was markedly less, although it was above 2,000 grams.

#### PLANT ASSOCIATIONS

*Anniella pulchra nigra* occurs more generally in stable sand dunes than in moving or strand dunes. The floras of these two types of sand dunes are strikingly different. Table 9 lists the majority of the

TABLE 9. Plant associates of *Anniella pulchra nigra* in Monterey County; a, abundant; m, moderately common; s, sparse.

	Moving dunes	Stable dunes	Carmel	Point Pinos, mainland	Point Pinos, islet	Castroville	Moss Landing	Watsonville
Pinaceae								
Pinus radiata		s	a	a				
Cupressaceae								
Cupressus macrocarpa		s	a	a				
Graminae								
Bromus rigidus		m	s					
Bromus carinatus				s				
Elymus mollis							m	
Hordeum nodosum				s				
Ammophila arenaria	a							a
Polygonaceae								
Eriogonum parvifolium		D		a				
Chenopodiaceae								
Atriplex californica		Su		a				
Nyctaginaceae								
Abronia latifolia	a	m	a	a		a	a	m
Aizoaceae								
Tetragonia expansa (?)				s				
Mesembryanthemum aequilaterale	m			m		m	m	
Caryophyllaceae								
Spergula arvensis				a				
Papaveraceae								
Eschscholtzia californica var. maritima				a		m		
Cruciferae								
Thelypodium lasiophyllum					m			
Leguminosae								
Lupinus arboreus		D	a	a		a	m	m
Melilotus indica				s				
Astragalus menziesii				s	a			
Frankeniaceae								
Frankenia (?)				m				
Onagraceae								
Oenothera spiralis		m	a	a		a		m
Convolvulaceae								
Convolvulus soldanella	m					m	m	m
Hydrophyllaceae								
Phacelia distans				a				m
Boraginaceae								
Amsinkia spectabilis				a				
Scrophulariaceae								
Castilleja latifolia		Su		m		m	m	
Compositae								
Asteraceae								
Ericameria eriocoides		D	m	m		a	a	m
Ambrosiaceae								
Franseria bipinnatifida	m		s	m	s	a	a	a
Heleniaceae								
Baeria uliginosa				s				
Eriophyllum								
staechadifolium var. artemisiaefolium		D		s				
Anthemideae								
Artemisia pycnocephala		Su	m	m				m



FIG. 13. Surface of the second islet off Point Pinos. The dark vegetation is *Eriogonum* growing in the shell mound. In 1939-1940 sixty-two black limbless lizards were found here.

species of plants of the Monterey Peninsula at localities where *Anniella* occurred. At Castroville and Moss Landing in the moving dunes there is another lupine (probably *Lupinus tidestromi*). The dominants (D) and subordinates (Su) (Cooper 1936) are marked in the column of stable dune plants. This tally is complete for the islet off Point Pinos and nearly complete for the other localities.

*Anniella pulchra pulchra* occurs at Antioch, Contra Costa County, in the oak-grass covered sand hills. There the lizards migrate into grape vineyards where they are occasionally plowed out. The oak-grass association is characterized by *Quercus agrifolia*, annual grasses, *Erodium*, *Godetia* and *Echinocystus*. In local areas these hills are dune-like and are characterized by cover of *Lupinus arboreus*, *Oenothera palida* and *Eriogonum nudum* (?).

At Cantua Creek, Fresno County, the silvery lizards are in cottonwood-grass association.

On the alluvial fan near Claremont, Los Angeles County, the lizards occur in sage-chamise association.

## POPULATION

### POPULATION DENSITY

The population density of the limbless lizard at most collection stations is low. The majority of localities of collection are represented by one or two specimens. The three areas that I have examined critically show different population densities.

Antioch, *A. p. pulchra*. The area examined is roughly a half mile wide and extends along the south shore of the San Joaquin River for three miles, east of the city of Antioch, Contra Costa County. Within this area there are several foci of occurrence. The lizards were all taken from under boards, logs or other litter. Since the distribution of such cover is not uniform, the intensity of collecting effort was not uniform over the area, but concentrated in the region of such litter. In one area atop a small hill seven lizards were taken within one hundred feet in one and one-half hours of search on February 11, 1940. One lizard was found under some of the same cover on June 23, 1940. A total of 30 silvery limbless lizards have been taken from these sand hills.

Castroville, *A. p. pulchra-nigra* intergrades. Two

miles west of Castroville in the sand dunes paralleling Monterey Bay is a colony of intergradient limbless lizards. The majority of the collecting effort has been expended on an area approximately one hundred by two hundred feet, behind a fruit packing shed. The sand there was littered with many boards, timbers and logs. On March 23, 1940, six lizards were taken in twenty minutes. The lizards occur to the seaward also, where the dunes are devoid of logs and timbers. In the driftwood zone high on the beach lizards were found under the more landward of the driftwood piles. A total of 26 lizards was taken from the entire area which is about two hundred by five hundred feet.

Second Islet off Point Pinos, *A. p. nigra*. This islet has been cut off from the mainland of Point Pinos by tidal action. The top is approximately one hundred feet square (Figs. 13, 14). Sixty-two liz-



FIG. 14. Surface of the second islet off Point Pinos, Monterey County, California. Collection sites of black limbless lizards in March, 1940, are indicated by dots, in May, 1940, by triangles. Connected circles and triangles show the minimum distances traveled by individual lizards in two months. The rectangle locates the site of liberation of black and silvery limbless lizards in September, 1940.

ards were found here between August, 1939, and May, 1940. The known population of *nigra* was forty-five individuals on September 11, 1940, when ten *A. p. pulchra* were liberated there. During 1939-40 there were at least sixty-two lizards on the island, or roughly one lizard to every 161 square feet.

On March 19-21, twenty-eight lizards were found. Twenty-seven of these were marked and liberated at the exact spots of capture. On May 19-21 the same area was examined with the same intensity as in March. Of the twenty-seven lizards found in March only ten were found in May. In addition twenty-two lizards were taken which had not been found in March. The ten lizards had moved an average of 8.67 feet (from 1.87 to 27.5 feet). The movements in two months indicate sedentary habits.

The stations of collection of the limbless lizard indicate localized populations. In all probability the lizards occur in these local areas and are not generally distributed over their entire range. Some of these population areas in addition to those discussed above are: Cantua Creek, Fresno County (thirty miles southwest of Mendota); Claremont, Los Angeles County; San Diego, San Diego County; and the islands off Lower California—Los Coronados, Todos Santos, and San Geronimo (*A. geronimensis*).

#### BARRIERS TO DISPERSAL

As shown by the movements of the ten lizards mentioned, the rate of emigration is slow. They are constantly moving about, however, as burrow systems in the laboratory were constantly changed and individuals were taken in the field from under the cover where specimens had been taken months before.

The major limiting factor in distribution is moisture, both extremes preventing the extension of range. The San Joaquin delta region is as efficient a barrier as are the dry sands of the desert. The lizards penetrate as far as possible against these barriers to within a few feet of the water of the delta region and into the few oases at the edge of the deserts (Jacumba, Yaqui Well and La Puerta in San Diego County).

The temperature of the ground is the second limiting factor. Temperatures over 40° C. are lethal for the lizards. Hot sands of the desert thus form a barrier. When the ground temperature was below 12° C. in the laboratory, the lizards were not active. They were apparently uninjured by a temperature of 4° C. for one day. However, prolonged low temperatures which are common in some regions form a barrier. This barrier is especially severe in high mountains where the ground is frozen for long periods.

The soil conditions of the surface of the ground form the third factor. The lizards can penetrate firm soil of a sandy or loamy texture but not clay or adobe. The pressure required to force the head of a lizard through unconsolidated sand is less than 10 grams, whereas compacted sand may require more than 2,000 grams pressure. The region of sand in

which lizards were found offered up to 1,000 grams resistance. Thus the more friable the soil, the easier it would be for the limbless lizard to burrow.

The fourth limiting factor may be the vegetation of a given terrain. The oak-annual grass association and the lupine-stable dune association are both favorable. The perennial grasses, such as *Ammophila arenaria*, may be a limiting factor because of the dense turf they establish.

Agricultural practices may be mentioned here, not because they are a limiting factor to distribution, but because they are destructive to the population that is present. Farmers uncover the lizards while plowing near Antioch and along Monterey Bay.

#### SUMMARY

1. The family Anniellidae includes only the genus *Anniella*, which has been derived by specialization and degeneration from the Anguillidae. The genus contains two species, *Anniella geronimensis* and *Anniella pulchra*. The latter is now divided into the subspecies *A. p. pulchra* and *A. p. nigra*.

2. The limbless lizards eat the larvae of insects, small adult beetles and spiders. They feed on the surface of the ground or just below it, usually in the leafy litter under bushes.

3. *Anniella* is ovoviviparous, the young being born in September, October or November. There are from one to four young produced at one time (an average of 1.7 embryos were taken from eight females).

4. There are four age groups: young of the year, immature, subadult and breeding adult. These lizards are probably two or three years old before they breed.

5. Before shedding, the black lizards become light blue. Ecdysis follows this stage in two to six days, and is usually completed two or four days later. Moisture is essential to shedding. The blue pre-shedding color is evident only on the longitudinal stripes in the silvery lizards.

6. *Anniella* is parasitized by a nematode (Oxyuroidea: Theladors) in the colon, and a cestode (Anoplocephalinae: Oochoristica) in the stomach and intestine. No external parasites have been found.

7. Locomotion is accomplished only by lateral undulations of the body. Progression is chiefly underground.

8. The special senses which are apparently especially well developed are smell and touch. *Anniella* shows no phototropisms.

9. These fossorial lizards are usually found in a temperate climate, in the Upper Sonoran and Transition Life-zones. They usually occur in sand hills or in rolling country in fine-textured soils. Cover is essential and is usually in the form of bushes, leaf droppings beneath bushes, boards, or debris.

10. The activity of *Anniella* is controlled by temperature. The optimum temperature is from 15° C. to 25° C. Below 13° C. the lizards are inactive, although they can stand a temperature of 4° C. Above 40° C. is lethal. The lizards bask in the warm sand



during the day. They are active and feed in the afternoon and evening.

11. Moisture is essential to the existence of *Anniella*. The optimum condition is dry sand overlying damp sand (of soil moisture from 2 to 8 per cent the total weight of the raw soil sample), where the lizards can move freely from one to the other. Saturated soil is not habitually entered.

12. The usual depth of habitation of the limbless lizard is from one to four inches. The animals will penetrate as deep as the moisture and the compactness of the earth will permit, however.

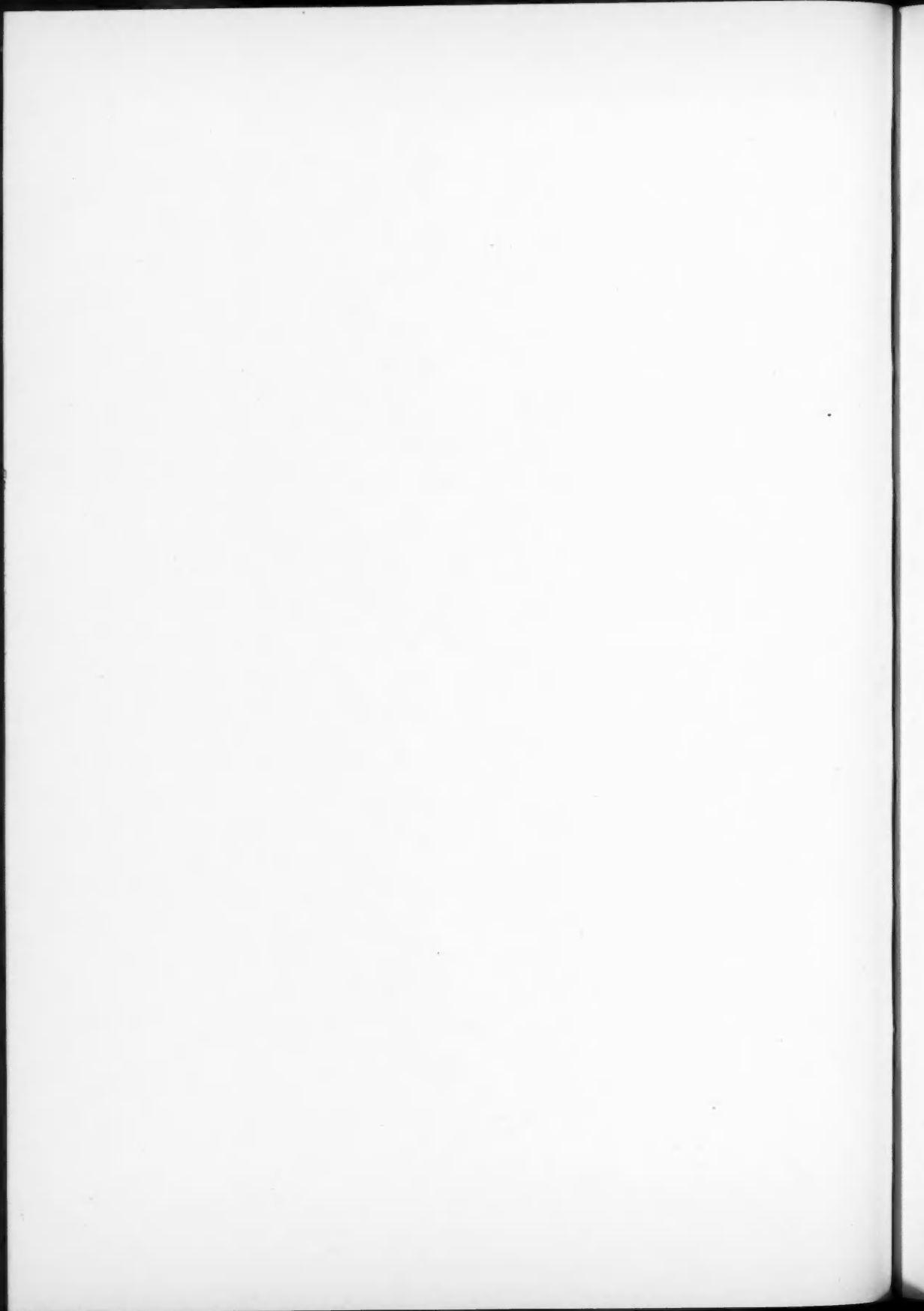
13. *Anniella* is closely dependent on plant associates. Vegetation provides cover, retains moisture near the surface of the ground and directly or indirectly supports the soil fauna on which the lizards feed.

14. The limbless lizards apparently occur in localized areas. They are sedentary, the individuals not moving far (from 1.8 to 27.5 feet for ten lizards in two months time).

15. Moisture is a major factor limiting their distribution. Other factors are temperature, soil textures, vegetation and agricultural practices.

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ECOLOGICAL STUDIES OF THE PAUROPODA  
OF THE DUKE FOREST

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# ECOLOGICAL STUDIES OF THE PAUROPODA OF THE DUKE FOREST

## INTRODUCTION

The Pauropoda, which constitute a class of microscopic progoneates (Pocock 1893), are distinguished from other "myriapods" by the presence of branched antennae, eleven body segments, and nine pairs of legs in the adult (excepting Decapauropus which has 12 body segments and ten pairs of legs, Remy 1931).

The small size of these interesting creatures has undoubtedly concealed their presence, so that many zoologists do not consider them to be common. Some, however, believe them to be rather generally distributed with the exception of the arctic, antarctic, and desert regions. Wherever found, they inhabit dark, slightly damp niches; under decaying logs; under stones and lumps of clay (Hansen 1902, Hilton 1928, 1930); among leaf litter, and in the soil itself. Their habitat seems to indicate that they are of the same economic importance as is credited to the other "myriapods," that of transforming the litter into soil, although little is known about their feeding habits.

Numerous but scattered ecological data are recorded in literature relative to classes Chilopoda, Diplopoda, and Symphyla, but such information is extremely scanty with respect to the Pauropoda. The present paper attempts to develop an understanding of some of the interacting forces which result in communities of Pauropoda; to extend their geographical range, and to bring together the literature pertaining to these minute animals.

At least three of the six known families of Pauropoda are represented in the Duke Forest. As a result of this investigation, five new species (Starling 1943), and one established species are reported as follows:

### Pauropodidae

*Pauropus carolinensis* Starling, 1943

*Pauropus dukensis* Starling, 1943

*Pauropus causeyae* Starling, 1943

*Stylopauropus* n. sp. Starling, 1943

### Brachypauropodidae

*Brachypauropus pearsei* Starling, 1943

### Eurypauropodidae

*Eurypauropus spinosus* Ryder, 1879

The procedure in this problem of investigating the ecology of the pauropods of the Duke Forest involved: (1) a quadrat study of soil samples to show; number, vertical and horizontal distribution of pauropods with respect to temperature, ionization, moisture, soil, and cover types; (2) collections from various localities of the Forest to determine the species present; (3) periodic observations of specimens in constant temperature cabinets to determine

optimum and extreme temperatures and their effects on activity; (4) studies on the life history, habits, and behavior of the most common pauropod in the Duke Forest, *Pauropus carolinensis* Starling.

The Duke Forest is dissected by numerous streams, and since the topography is slightly rolling, the surface water drains from the uplands rapidly, with the exception of a few poorly drained flats (Korstan & Maughan 1935). The elevations in the forest range from 280 to 650 feet above sea level. The air temperatures range from an annual average minimum of approximately 48° F. to an annual average maximum temperature of approximately 71° F., and seldom fall below zero (Gray 1941). Severe weather lasts only a few days at a time and the soil seldom freezes to more than a few inches in depth. Periods of drought often occur that last for as long as a month and a half. Table 1 gives the mean monthly temperatures and precipitation for Durham, N. C., for the specific months during which the material for this study was collected.

The author wishes to express his sincere appreciation to Dr. A. S. Pearse, who suggested and directed this study; to Dr. Nelle Bevel Causey, who identified the chilopods and diplopods; to Dr. A. E. Michelbacher, who is identifying the symphylans; to Dr. T. S. Coile, who offered valuable suggestions and criticisms; and to the Duke University Zoology Staff, each of whom contributed advice and inspiration.

## METHODS

### POPULATION STUDIES

Various methods which have been employed in the study of microorganism populations have been reported by Tullgren (1918), Waksman (1927), Bornebush (1930), Tragardh (1933), and Jacot (1936). No single work has previously reported on the study of pauropod populations.

TABLE 1. Air temperature and precipitation in the Duke Forest, 1940-41.

	Mean Temperature Degrees Centigrade		Precipitation Inches	
	1940	1941	1940	1941
January.....	1.5	3.4	3.21	1.54
February.....	6.5	2.8	2.66	1.26
March.....	8	6.7	3.32	3.00
April.....	14	16.1	3.06	2.01
May.....	18.5	20	4.88	1.76
June.....	25	23.9	2.63	1.85
July.....	25	26.2	2.53	5.24
August.....	25	25.6	7.42	0.91
September...	20	23.3	0.55	1.72
October.....	15	25	0.48	0.85
November...	9	10	5.86	0.40
December...	7	6.7	2.29	2.20



TABLE 2. Temperature of air, litter, and soil; date; and time of day as recorded for visits to each station.

	Time of Day	STATION 1				Time of Day	STATION 2				Time of Day	STATION 3				Time of Day	STATION 4			
		Temperature (°C)					Temperature (°C)					Temperature (°C)					Temperature (°C)			
		Air	Litter	1-2" Soil	3-5" Soil		Air	Litter	1-2" Soil	3-5" Soil		Air	Litter	1-2" Soil	3-5" Soil		Air	Litter	1-2" Soil	3-5" Soil
1940																				
November 17	12:40	12	9	6	5	12:10	13	10	8	7	11:00	12	8	7	5	11:40	12	9	7	5
November 21	4:45	18	14	10	9	3:00	19	14	11	9	3:45	19	15	9	8	3:30	19	14	11	10
December 3	2:30	5	5	6	6	12:20	4	6	6	7	11:30	5	5	7	7	11:45	5	7	7	7
December 8	11:00	8	5	5.5	5.5	9:45	6	5	6	7	10:35	8	6	5.5	5.5	11:20	8	5	5	5.5
1941																				
January 7	3:45	4	5	6.5	6.5	2:00	3	4.5	5	7	2:30	4	5	5	5	3:15	4	6	5.5	5.5
February 9	11:15	-2	2	4	5	10:15	-2	2	5	5	9:30	-3	0	3	3	8:45	-3	1	4	5
February 16	11:40	4	4	5.5	5.5	10:15	3	5	5.5	6	9:45	9	4	5	4	9:20	2.5	3.5	5	5
March 2	11:00	10	3	3	3	9:45	4	4	4	4	10:15	6	4	4	4	10:40	10	4	4	4
April 23	11:00	13	12	12	12	9:00	13	12	12	9:45	13	12	12	12	10:30	13	12	12	12	12
May 19	9:15	23	17	15	15	10:15	23	16	15	15	11:00	24	18	15	15	11:45	24	17	15	15
June 30	12:00	30	23	22	21	10:00	27	23	21	20	11:00	29	23	22	22	11:30	30	25	23	22
July 9	12:00	25.5	23.5	20.5	20	10:15	25.5	23	20.5	20	10:45	26	23.5	21	20.5	11:25	25.5	23	21	20
August 26	12:30	29	24	22.5	21.5	11:45	28.5	23.5	22	21.5	10:20	27	23.5	22	21	11:00	27	23	22	21
September 30	10:30	19.5	19	19	19	9:00	18	18.5	19	19	9:45	18.5	18.5	19.5	19.5	10:15	19	19	19.5	19.5
October 31	4:15	22	18.5	16	16	3:45	23	19	16	15.5	2:30	23.5	20.5	17	17	3:00	23.5	19	17	16
November 22	11:15	9.5	10.5	11.5	11.5	10:20	7	8	10	12	9:30	5	8	10	11	10:00	7	9	10	10
November 28	11:20	18	11	10	9	9:45	11	9	8.5	8.5	10:15	17	10	9.5	9.5	10:45	18	11	10	10
December 22	4:00	10	8	8	7	2:00	10	9	8	8	2:45	10	9	7	7	3:30	10	9	7	7
1942																				
January 6	12:00	-3	3.5	6	7.5	9:45	-4	3	6	7.5	10:15	-3	4	6	7.5	11:10	-3	4	6	7.5
January 13	4:00	10.5	7	5	5	3:30	11	7	5.5	5	2:20	13	7	5	4.5	3:00	13	6.5	5	4.5

The following description embodies the procedure used in the present investigation. Four stations, each one hundred yards square and subdivided into one hundred equal plots (Fig. 1) were staked off in suitable localities in the Durham Division of the Duke Forest. The principal overstory of trees in two of the stations was pine; in the other two stations it was oak. Each station is shown in Figures 2a, 2b, 3a, 3b and may be characterized as follows:

#### Station 1 and 2.

Ninety-five-year-old short-leaf pine (*Pinus echinata* Miller) stand; sandy soil; litter mainly of pine needles with scattered oak and dogwood leaves; A<sub>0</sub> was 2-3 in. thick with L layer approximately 0.75 in. thick, F layer 1.5 in. thick, and H layer 0.25 in. thick; A<sub>1</sub> was 2-2.5 in. thick with light grayish and friable soil well filtered with organic material.

#### Station 3 and 4.

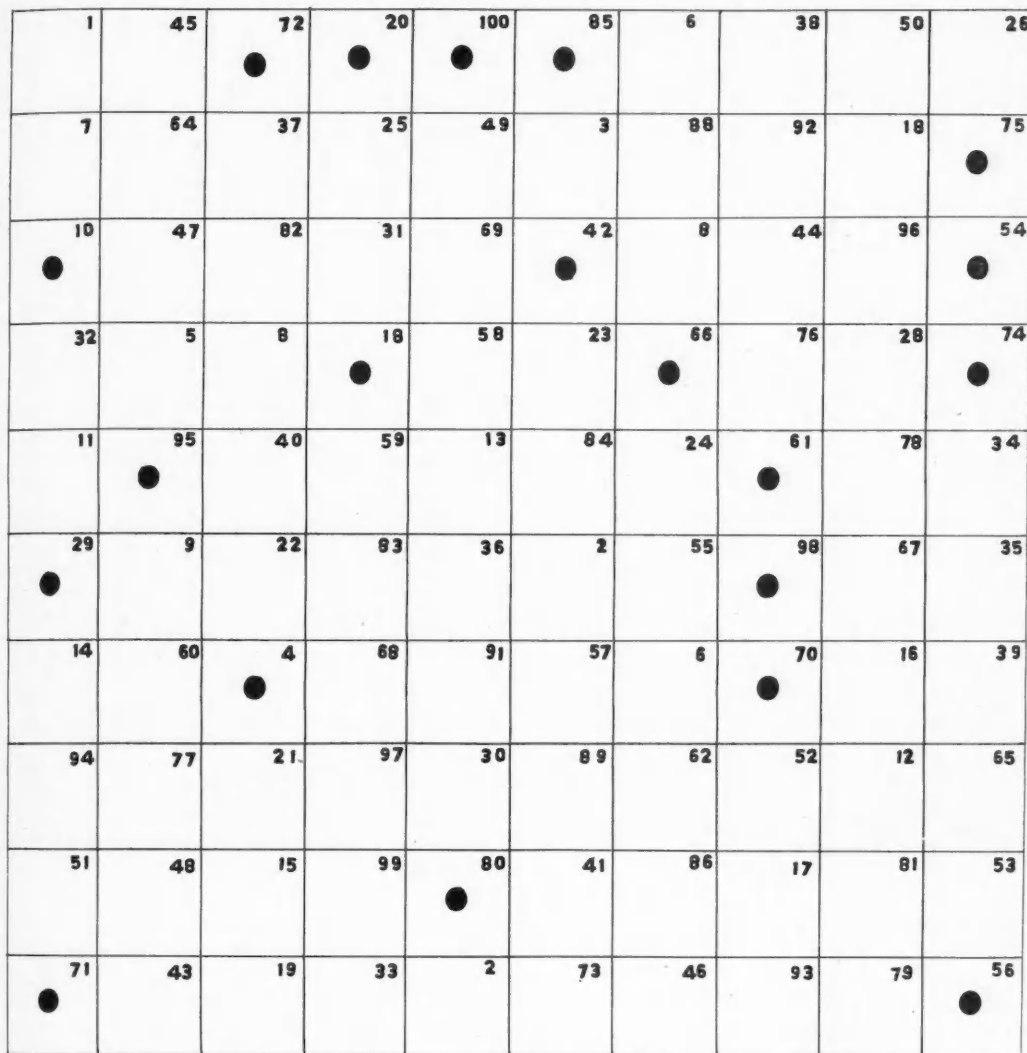
Uneven aged hardwood with oak (*Quercus alba* Linnaeus, *Quercus borealis maxima* Ashe, *Quercus velutina* La Moreh) predominating; clay loam; litter principally of oak and dogwood leaves; A<sub>0</sub> was 1-2 in. thick with L layer approximately 0.5 in. thick, F layer 1 in. thick, and H layer 0.5 in. thick; A<sub>1</sub> was 1-2 in. thick with relatively little organic matter.

To obtain quantitative estimates of pauropod populations within given localities, the animals were extracted from measured volumes of soil samples. Random samples were obtained from as near the center of each plot as could be approximated. Three

samples (A, B, and C) were taken from the same corresponding plot of each station during a period of from three to four hours. The first (A) consisted of litter and humus scraped from a square foot area; the second (B) consisted of soil taken from one and two inches in depth; and the third (C), of soil from three, four, and five inches in depth. Samples were obtained from the same vertical plane. To secure a soil sample a galvanized iron cylinder (Figs. 4, 5) five inches in diameter (two inches in depth for sample B, three inches in depth for sample C) was capped and pressed into the soil. The steel cap is shown in Figure 9. The soil was scraped from one side of the cylinder and the cutting edge of a tin tray (8.5 in. square, Fig. 7) was inserted under the lower edge until the cylinder rested entirely on the tray. The sample could then be easily removed to the laboratory.

The air temperature at about a foot above the ground and the soil temperature for each level where samples were recorded at the time each sample was taken. Table 3 gives the actual air and soil temperatures recorded for each field trip and each sample taken from Duke Forest. In addition, the hydrogen-ion concentration was recorded with a Hellige soil tester. Samples of soil from each level were taken to the laboratory in tightly closed can (Fig. 6) and dried at a temperature of 95° C. in order to determine the moisture content.

The apparatus used in extracting the pauropods, as well as numerous other microorganisms, from soil samples was modelled on that of Jacot (1936) (Fig.



1

FIG. 1. Diagram of a station (100 ft. square) with plots (each 10 ft. square). The circles indicate plots from which samples were taken.

10). The principle involved is that of driving the animals downward by the application of light, heat, and desiccation. A battery of twelve funnels, each equipped with sieves, was used during the experiments. A gooseneck lamp, with a 60-watt bulb, for each funnel produced a sufficient amount of light and heat. Temperatures in the funnels never rose above 40° C.

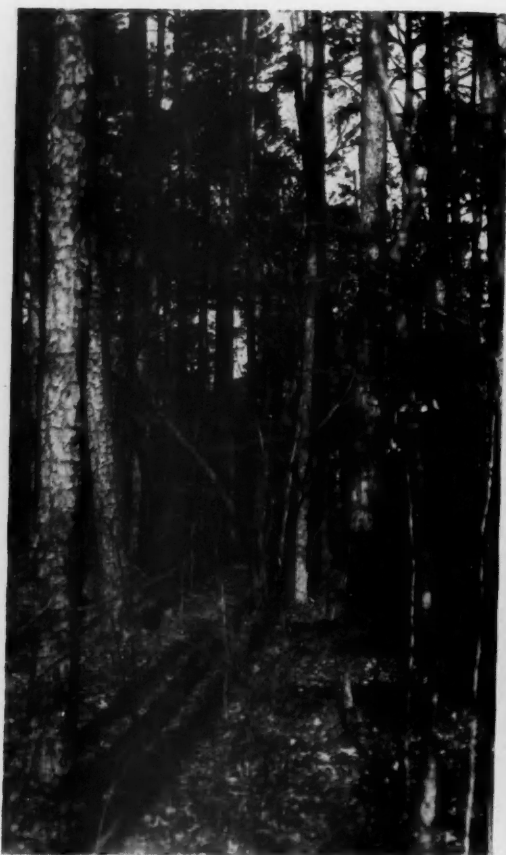
Most of the pauropods along with the other animals left the samples within a period of 24 hours after soil or litter was placed in a funnel. Some, however, lingered as long as three days. Tapping

the funnels gently at intervals seemed to accelerate the dropping down of animals. The funnels concentrated catches, which were directed into small vials of 70 percent alcohol and later sorted. Animals were driven from 240 samples of litter and soil.

To obtain specimens alive the same apparatus was used; the animals were allowed to fall into a watch-glass of water instead of alcohol. As the surface tension of the water was great enough to support these minute pauropods, they were easily picked from the surface with a brush or a needle, preferably the latter.



A



B

FIG. 2. Short-leaf pine stands, approximately ninety-five years old, growing in sandy soil. A, Station 1; B, Station 2.

#### TEMPERATURE TOLERATIONS

A constant temperature apparatus (Fig. 11) used for experiments consisted of six individual cabinets, each capable of temperatures varying from approximately  $42^{\circ}\text{C}$ . to  $-30^{\circ}\text{C}$ . with a fluctuation of not more than a  $\pm 0.5^{\circ}\text{C}$ .

Fifty specimens, ten to each of five stender dishes were placed in each of the six cabinets for a period of thirty days. The temperature of the cabinets ranged from  $12^{\circ}$  to  $33^{\circ}\text{C}$ . Later a second series of temperatures ( $8^{\circ}$  to  $-12^{\circ}\text{C}$ .) were maintained for 30 days. This time only twenty specimens were used in each cabinet.

#### REARING DISHES

The rearing dishes (Fig. 8), also used for storage dishes, were modifications of those devised by Michelbacher (1938) and were made by pouring "muck plates" (10 parts plaster of Paris, 3 parts soil, and 1 part bone black) into stender dishes to a depth of about  $\frac{1}{4}$  of an inch. Before setting took place a

glass tube slightly shorter than the depth of the dish and plugged with bits of cheese cloth was placed, standing vertically, in the muck. The cheese cloth was kept saturated with distilled water to keep the animals moist. Bits of decaying leaves were added from time to time and appeared to serve as a source of food. The surface of the plate was dampened with 1-100 parts of copper sulfate solution to prevent an excess growth of molds. The bone black offered a dark background on which the animals, eggs, and molted skins were easily visible. Since in some cases pauropods were kept alive for as long as seven months, conditions in the dishes must have been favorable.

#### MOUNTING

Only specimens that were collected alive were used for mounts. To preserve these animals in an extended position a specimen was first dropped into a rather strong, caustic solution and boiled for at least two minutes. After a thorough washing in water a specimen was drawn into a pipette, placed on a



A



B

FIG. 3. Uneven aged oak stands, growing in clay soil. A, Station 3; B, Station 4.

slide, and the adhering water absorbed away. A drop of lactic acid was then added and allowed to penetrate the skeleton. When all of this was absorbed away from around the specimen a drop of a modification of Berlese's clearing and mounting medium was added and a cover glass applied. Fuschin and eosin were used at times but unstained mounts proved more satisfactory. The proportions of the constituents of the mounting medium used were as follows:

Gum arabic, white crystals.....	12 gr.
Chloral hydrate.....	20 gr.
Distilled water.....	20 cc.
Glycerine, conc.....	6 cc.

#### MICROSCOPIC EXAMINATION

A binocular microscope was used in examining living material. A strong light was needed to properly illuminate the animals. A satisfactory type of light was given by Spencer's Universal microscope lamp (6.5 v., 1.7 amp.) which tended to focus the light on the desired area. A microscope was always

used in examining mounted material. All drawings were made with the aid of a camera lucida.

#### OBSERVATIONS AND RESULTS

##### BEHAVIOR

Cultures in rearing dishes were valuable in that they afforded an opportunity to observe some of the habits of the pauropods under laboratory conditions. These small "myriapods" are without doubt negatively phototropic (Verhoeff 1934); such responses are seemingly less strongly developed in *Eurypauropus spinosus* and *Brachypauropus pearsei* than in any Pauropodidae observed. In other words, those species were not nearly so eager to find a dark crevice in which to hide.

There is likewise developed among the pauropods a positive response to moisture. This hydrotropic response seems to be positive only in approaching optimum conditions. In supraoptimum conditions, animals seek drier levels. When the rearing dishes were allowed to "dry out" somewhat, animals dis-

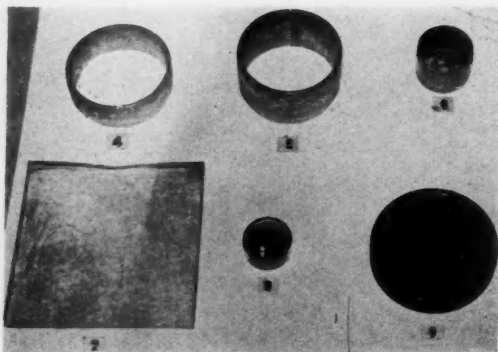


FIG. 4. Galvanized iron cylinder (5 in. in diameter and 2 in. in depth), with which sample B was secured from the soil.

FIG. 5. Galvanized iron cylinder (5 in. in diameter and 3 in. in depth), with which sample C was secured from the soil.

FIG. 6. Can used in obtaining samples of soil to determine its moisture percentage of oven-dry weight.

FIG. 7. Tin tray (8.5 in. square), which was inserted under the cylinders to remove the sample from the ground.

FIG. 8. A rearing dish.

FIG. 9. Steel cap used to cover the cylinders as they were driven into the soil.

appeared into crevices at lower depths. However, as soon as a few drops of water were added to a plate, pauropods immediately reappeared on the surface and traveled toward moistened areas. If a plate

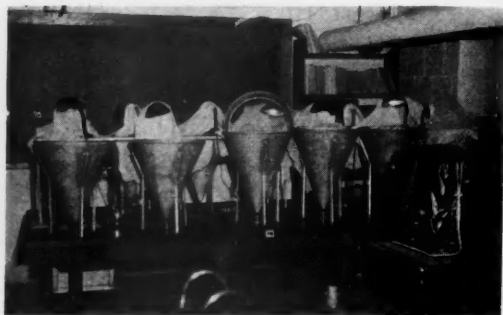


FIG. 10. Battery of funnels used in extracting pauropods from soil samples.

were saturated with water, animals would retreat to higher and drier levels and even climb the sides of a glass dish.

It was observed in the forest that during droughts pauropods were concentrated in sunken areas, the moisture of which was conserved by a deep layer of litter, whereas in unprotected areas they appeared to be nearly or wholly absent. This seemed to indicate that as the areas dried out the animals were forced to migrate to more favorable places and finally resulted in concentrations in only areas that were moist enough for them to survive. During extremely wet seasons, specimens were rare.

Records indicate that the favorite haunts of pauropods are under stones, moss, clay, and in accumulations of decomposing organic material in wooded

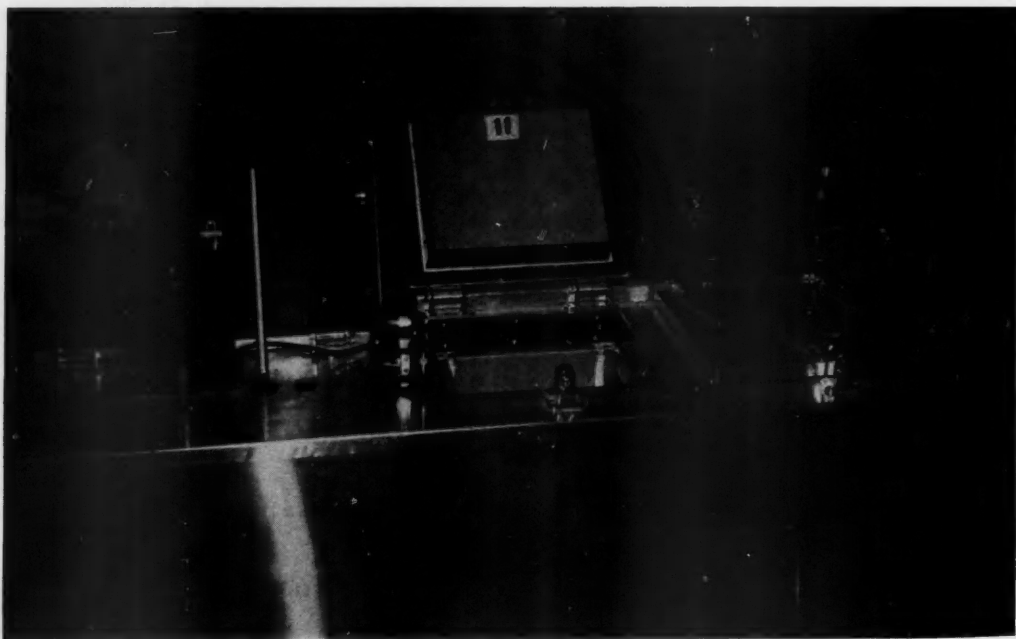


FIG. 11. Constant temperature apparatus with six cabinets.



areas where there is sufficient moisture (Lubbock 1866, Ryder 1879, Latzel 1880-84, Kenyon 1895, Hansen 1902, Harrison 1914, Hilton 1929-34, Remy 1930-40, Verhoeff 1934, Bagnall 1909-35). One species is recorded as inhabiting sub-littoral regions (Bagnall 1935, Remy 1935).

Responses to contact stimuli may be various. When *Pauropus carolinensis* was touched gently with a dissecting needle, the stimulus being applied to either the long sensory bristles or to the trunk, the animal usually darted forward. If the animal was continuously agitated, its body, legs and antennae would become rigid in much the same manner as an opossum feigns death.

If air is forced from a dropper in the direction of a pauropod, it may dart forward or it may crouch in a position such that its body is telescoped to about one-half its normal length and remain shortened until the stimulus is removed or sometimes for even a longer time.

Another type of behavior often observed among the Pauropodidae studied was that of cleaning antennae and feet (Lubbock 1866, Harrison 1914). Harrison has vividly described the process: "They spend a great deal of their time cleaning their appendages, commencing with the antennae, which are hauled down by the vigorous curling of the corresponding first leg about them, and drawn rapidly across the mouth; and proceeding on to each pair of legs in turn, the limb being systematically washed from coxa to tarsus. The attitude assumed, in cleaning the extended hinder limbs is amusingly reminiscent of the same process in the domestic cat."

Another characteristic habit often observed among *Pauropus carolinensis* is that in which the animal allows its body weight to be supported by the posterior three or four pairs of legs, with the head and anterior portion of the body elevated for observation. The behavior is of great assistance to the collector since the animals in this elevated position are more easily distinguished from the other animals that might be present on a water surface. Also a needle can easily be inserted beneath them and the pauropods readily attach themselves to it.

When *Eurypauropus spinosus* is slightly stimulated with a dissecting needle, the animal may hasten along (not dart) or it may settle down to the surface of a plate. It is protected by its strongly chitinized terga. If the animal is forced on its side, its legs and antennae become rigid and it feigns death (Ryder 1878).

*Brachypauropus pearsei* seems to detect an approaching needle, since even before the instrument touches either the long sensory bristles or the trunk, the animal tilts its terga in the direction of the oncoming stimulus, and settles close to the substrate. Like the others, this species "plays 'possum." It reacts to air blown in its direction in a similar fashion as does *Pauropus carolinensis*.

As has been pointed out (Latzel 1884), pauropods may be divided into two groups on the basis of their

locomotion, the quick and the slow types. Of the three families under observation during this study, Pauropodidae would be included in the former, whereas Eurypauropodidae and Brachypauropodidae would be considered slow.

The lateral structures of the leg claw deserve mention because they constitute the adhesive apparatus by which the animals are able to move up a vertical glass surface (Verhoeff 1934). Such behavior was observed only among the Pauropodidae.

Both the slow and quick types appear to be gregarious (Harrison 1914). In rearing dishes several pauropods could be found congregated under a twig or a leaf. Furthermore, in the forest, when conditions appeared to be favorable in almost any situation, animals seem to be in groups since a funnel would yield perhaps a hundred or more specimens from one sample; whereas another sample taken several feet away would contain none. Possibly the animals were seeking optimum conditions since not one time were animals observed showing any concern over the presence or absence of another of its kind. Though on several occasions *Pauropus carolinensis* was observed avoiding a pseudoscorpion or a mite.

The rhythmical movements of a pauropod's antennae immediately attract the attention of an observer. When an animal is in motion the antennae move simultaneously from one side to the other. But when it comes to rest, each antenna begins working alternately, and instead of the side to side motion, first one then the other is thrown anteriorly. While an animal appears to be feeding the antennae are not in motion; the peduncle of each rests on the lateral surface of the head and points postero-laterally.

Schmidt (1895) suggested, relative to the breeding habits of the pauropods, that a "true coitus" must exist and most likely the penes are inserted directly into the somewhat expanded opening of the oviduct, so that the sperm could fertilize the eggs upon their exit. This copulation process has not been actually observed. Parental care by a female has been recorded (Harrison 1914). She is known to guard her eggs until they hatch; thereafter, the young care for themselves.

#### FOOD HABITS

Little is known concerning the food of pauropods. Speculations suggest that the slowly moving species feed on decaying plant and animal material, whereas the agile types probably consume microscopic animals (Latzel 1884). Verhoeff (1934) found a species of *Pauropus* feeding on dead dipterans floating on a puddle. Harrison (1914) has no doubt that pauropods are humus feeders as he watched them "browsing" on particles of soil on which nothing in the way of food could be distinguished. The writer has seen *Pauropus carolinensis* eat myceli of molds that grew on decaying leaf particles. But in no instance did they appear to feed on dead animal material (Collembola, diptera, other pauropods) which was placed at their disposal.

## POPULATIONS

No previous records relative to Pauropoda indicate anything of a nature of population studies, but rather merely signify the presence or absence of a species in a locality. The methods of approach in the writer's studies is unique, in that quadrat studies and funnel collections have not been extensively used in "myriapod" population studies. It is interesting to note that of faunal surveys in which the procedure has been employed quite frequently, only one (Jacot 1935) speaks of the presence of pauropods. Considering their small size and the large number of other animals a funnel yields, it is quite possible, however, that they were overlooked, if present; or mistaken for the larvae of other types of animals.

In interpreting the data which follow it must be remembered (1) that since the forest stands were on different soil types, no specific correlations can be suggested with respect to either one of these two factors; (2) that a study of this type to be all conclusive should be based on samples taken over a period of several years; (3) that possibly the number of animals per unit volume is a basis from which the relative function of the species may be determined.

Tables 3, 4, 5, and 6 indicate the number and species of Chilopoda and Diplopoda; the number and families of Pauropoda; and the number of Symphyla collected during the writer's study.

TABLE 3. The number and species of Chilopoda and Diplopoda; the number and families of Pauropoda; and the number of Symphyla collected from sixty samples of soil from Station 1; a pine stand on sandy loam. November 17, 1940 to January 13, 1942.

Myriapods in A<sub>1</sub> Horizon

## Chilopoda

<i>Arenophilus watsingus</i> .....	1
<i>Garibius branneri</i> .....	2
<i>Garibius georgiae</i> .....	1
<i>Geophilus mordax</i> .....	2
<i>Gnathomerium unbraticum</i> .....	2
<i>Linotenia bidens</i> .....	1
<i>Lithobiid</i> (immature) .....	4
<i>Llanobius dur</i> .....	7
<i>Nadabius saphes</i> .....	2
<i>Nampabius mycophor</i> .....	4
<i>Nampabius</i> sp. ....	2
<i>Otocryptops sezespinosus</i> .....	5
<i>Pschymerium ferrugineum</i> .....	1
<i>Scolopocryptops nigrinus</i> .....	3
<i>Sigibius carolinus</i> .....	2

Total ..... 39

## Diplopoda

<i>Callipus lactarius</i> .....	2
<i>Parajulus pennsylvanicus</i> .....	7
<i>Polyxenus fasciculatus</i> .....	222
<i>Spirobolus marginata</i> .....	1

Total ..... 232

## Pauropoda

<i>Brachypauropodidae</i> .....	2
<i>Eurypauropodidae</i> .....	7
<i>Pauropodidae</i> .....	11

Total ..... 20

## Myriapods in 1-2" Soil

## Chilopoda

<i>Arenobius manegitus</i> .....	7
<i>Arenophilus watsingus</i> .....	3
<i>Geophilus mordax</i> .....	1
<i>Lithobiid</i> (immature) .....	2
<i>Sigibius carolinus</i> .....	1
<i>Sigibius reductus</i> .....	1

Total ..... 15

## Diplopoda

<i>Parajulus pennsylvanicus</i> .....	2
<i>Polyxenus fasciculatus</i> .....	26

Total ..... 28

## Pauropoda

<i>Pauropodidae</i> .....	110
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Symphyla ..... 17

## Myriapods in 3-5" Soil

## Chilopoda

<i>Arenophilus watsingus</i> .....	10
<i>Cryptops hyalinus</i> .....	1
<i>Geophilus mordax</i> .....	1
<i>Gnathomerium umbraticum</i> .....	1
<i>Linotenia fulva</i> .....	1
<i>Sozibius</i> sp. ....	1
<i>Theatops posticus</i> .....	1

Total ..... 16

## Diplopoda

<i>Polyxenus fasciculatus</i> .....	10
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## Pauropoda

<i>Pauropodidae</i> .....	58
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Symphyla ..... 11

TABLE 4. The number and species of Chilopoda and Diplopoda; the number and families of Pauropoda; and the number of Symphyla collected from sixty samples of soil from Station 2; a pine stand on sandy loam. November 17, 1940 to January 13, 1942.

Myriapods in A<sub>1</sub> Horizon

## Chilopoda

<i>Garibius</i> sp. ....	1
<i>Gnathomerium umbraticum</i> .....	1
<i>Lithobiid</i> (immature) .....	6
<i>Nampabius mycophor</i> .....	3
<i>Otocryptops sezespinosus</i> .....	1
<i>Pokabius</i> sp. ....	1
<i>Scolopocryptops nigrinus</i> .....	3
<i>Serrabius pulchellus</i> .....	2
<i>Startobius gracilis</i> .....	1

Total ..... 19

Diplopoda	
<i>Apheloria coriacea</i> .....	2
<i>Parajulus</i> (immature) .....	13
<i>Polyzenus fasciculatus</i> .....	105
Total .....	120
Pauropoda	
Pauropodidae .....	48
Symphyla .....	13
Myriapods in 1-2" Soil	
Chilopods	
<i>Arenophilus watsingus</i> .....	5
Lithobiid (immature) .....	1
Total .....	6
Diplopods	
<i>Polyzenus fasciculatus</i> .....	16
Pauropoda	
Pauropodidae .....	91
Symphyla .....	9
Myriapods in 3-5" Soil	
Chilopods	
<i>Arenophilus watsingus</i> .....	7
<i>Cryptops hyalinus</i> .....	1
<i>Linotenia bidens</i> .....	1
Total .....	9
Diplopoda	
<i>Parajulus</i> (immature) .....	1
<i>Polyzenus fasciculatus</i> .....	2
Total .....	3
Pauropoda	
Pauropodidae .....	42
Symphyla .....	16

TABLE 5. The number and species of Chilopoda and Diplopoda; the number and families of Pauropoda; and the number of Symphyla collected from sixty samples of soil from Station 3; an oak stand on clay loam. November 17, 1940 to January 13, 1942.

#### Myriapods in A<sub>0</sub> Horizon

Chilopoda	
<i>Gnathomerium umbraticum</i> .....	1
<i>Linotenia branneri</i> .....	11
Lithobiid (immature) .....	4
<i>Llanobius dux</i> .....	1
<i>Neolithobius mordax</i> .....	1
<i>Otocryptops sexspinosus</i> .....	1
<i>Paitobius</i> sp. ....	1
<i>Serrabius pulchellus</i> .....	1
<i>Sigibius carolinus</i> .....	1
<i>Sigibius reductus</i> .....	1
<i>Sigibius starlingi</i> .....	1
<i>Tidabius lilacius</i> .....	1
Total .....	25
Diplopoda	
<i>Callipus lactarius</i> .....	4
<i>Parajulus</i> (immature) .....	1
<i>Polyzenus fasciculatus</i> .....	72
Total .....	77

Pauropoda	
Brachypauropodidae .....	3
Eurypauropodidae .....	5
Pauropodidae .....	87
Total .....	95
Symphyla .....	41
Myriapods in 1-2" Soil	
Chilopoda	
<i>Arenophilus watsingus</i> .....	4
<i>Gnathomerium umbraticum</i> .....	2
Lithobiid (immature) .....	1
<i>Pachymerium ferrugineum</i> .....	1
Total .....	8
Diplopoda	
<i>Callipus lactarius</i> .....	2
<i>Polyzonium bivirgatum</i> .....	1
<i>Polyzenus fasciculatus</i> .....	23
Total .....	26
Pauropoda	
Pauropodidae .....	109
Symphyla .....	63
Myriapods in 3-5" Soil	
Chilopoda	
<i>Arenophilus watsingus</i> .....	1
<i>Gnathomerium umbraticum</i> .....	1
Lithobiid (immature) .....	1
Total .....	3
Pauropoda	
Pauropodidae .....	34
Symphyla .....	25

TABLE 6. The number and species of Chilopoda and Diplopoda; the number and families of Pauropoda; and the number of Symphyla collected from sixty samples of soil from Station 4; an oak stand on clay loam. November 17, 1940 to January 13, 1942.

#### Myriapods in A<sub>0</sub> Horizon

Chilopoda	
<i>Arenophilus watsingus</i> .....	3
<i>Garibius branneri</i> .....	2
<i>Garibius</i> sp. ....	2
<i>Gnathomerium umbraticum</i> .....	1
<i>Linotenia branneri</i> .....	1
Lithobiid sp. ....	6
<i>Nampabius mycophor</i> .....	1
<i>Otocryptops sexspinosus</i> .....	1
<i>Pachymerium ferrugineum</i> .....	1
<i>Serrabius pulchellus</i> .....	2
<i>Sigibius carolinus</i> .....	1
<i>Tidabius lilacius</i> .....	1
Total .....	22
Diplopoda	
<i>Callipus lactarius</i> .....	2
<i>Parajulus</i> (immature) .....	3
<i>Polyzenus fasciculatus</i> .....	74
<i>Spiroboles marginatus</i> .....	1
Total .....	80

Pauropoda	
Brachypauropodidae	2
Eurypauropodidae	9
Pauropodidae	57
Total	68
Symphyla	
Myriapods in 1-2" Soil	
Chilopoda	
<i>Arenophilus watsingus</i>	4
<i>Gnathomerium umbraticum</i>	1
Lithobiid (immature)	1
<i>Nedabius</i> sp.	1
Total	7
Diplopoda	
<i>Polyxenus fasciculatus</i>	7
Pauropoda	
Pauropodidae	43
Symphyla	33
Myriapods in 3-5" Soil	
Chilopoda	
<i>Arenophilus watsingus</i>	2
Lithobiid (immature)	1
Total	3
Pauropoda	
Pauropodidae	8
Symphyla	13

Of the total number (1,796) "myriapods" collected, 40.8 percent were pauropods, 33.4 percent were diplopods, 16.6 percent were symphylans, and 9.2 percent were chilopods. Of the pauropods collected 51.9 percent were from Station 1 and 2 where pine stands grew on a sandy loam soil.

By reducing the figures that represent numbers of "myriapods" collected to comparable units (number per square foot to a depth of 2 inches) it is then possible to indicate as in Figures 12 and 13 comparative relationships of "myriapod" populations with respect to both soil types and cover stands. The graph shows that in both cases the greatest number of pauropods were from the 1-2 in. samples. There were collected an average of 36.8 pauropods per unit volume from the sandy loam in the pine stands; and 27.9 from the clay loam in the oak stands. The A<sub>0</sub> horizon in the oak stands was seen to be five times more densely populated with pauropods than the same level in the pine stands. However, in the 3-5 in. samples of sandy loam from the pine stands the number of pauropods was 12 as compared to 5 found in the clay loam samples from the oak stands. If collections from all three layers are combined it may be estimated that in the oak stands there was an average yield of 1,672,704 pauropods per acre, as compared to 2,178,000 per acre in sandy loam of the pine stands.

It has been pointed out in a previous section of this paper that pauropods appeared to be positive to moist conditions, but avoid excessive moisture.

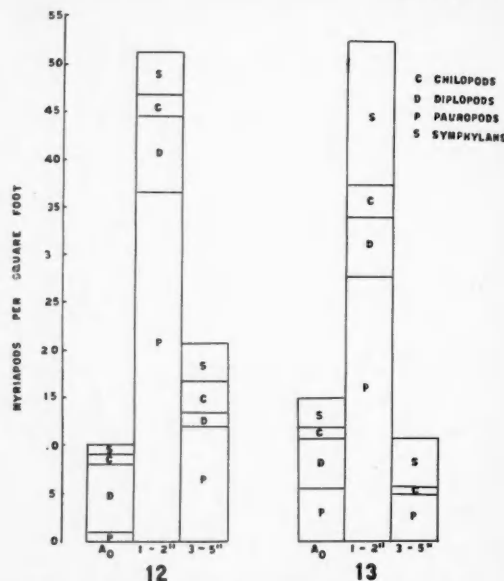
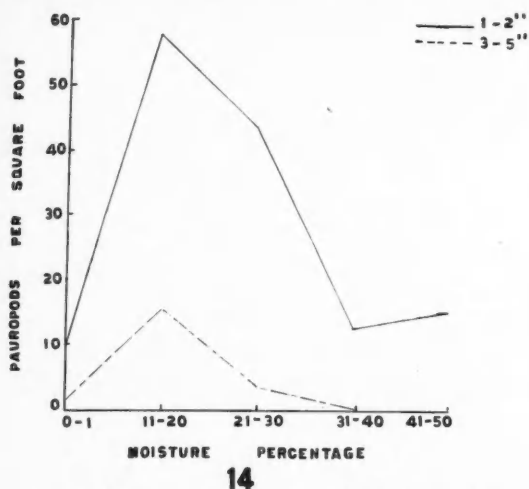


FIG. 12. Average number per sample of pauropods, diplopods, symphylans, and chilopods with relation to A<sub>0</sub> Horizon,  $\frac{1}{2}$  in. depth, and  $\frac{3}{4}$  in. depth of the pine stands on sandy soil.

FIG. 13. Average number per sample of pauropods, diplopods, symphylans, and chilopods with relation to A<sub>0</sub> Horizon,  $\frac{1}{2}$  in. depth, and  $\frac{3}{4}$  in. depth of the oak stands on clay soil.

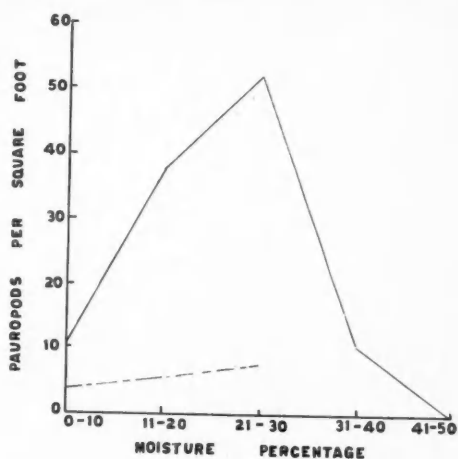
Figures 14 and 15 emphasize this correlation. In the sandy loam soil, the greatest number of pauropods per unit volume were found in samples at both the 1-2 in. and 3-5 in. depths when the moisture percentages were between 11 and 20. In the clay loam, which requires a greater percentage of moisture for saturation, the greatest number of pauropods were found in both sample depths when the moisture percentage was between 21 and 30. In both soil types it will be noted that the 1-2 in. depth was more densely populated with pauropods than the lower depths when the moisture percentages were the same.

Figures 16, 17, 18, and 19 indicate seasonal trends with regard to density of pauropod population. No doubt, more data would eliminate some of the fluctuations in the curves. Basing the percentage of seasonal increase or decrease on the annual average number of pauropods at the various levels sampled, one is able to note striking seasonal trends. In Figure 18 it may be seen that in the spring the greatest percentage of decrease is in the 3-5 in. level whereas there is an increase in the A<sub>0</sub> horizon. During the summer there is an increase in all levels; the greatest in the 1-2 in. level, and the next in the A<sub>0</sub>. There appears to be a decrease in the fall from the annual average number of pauropods in the lower depths; whereas there is a decrease in all levels in the winter, the percentage being least in the lowest level.



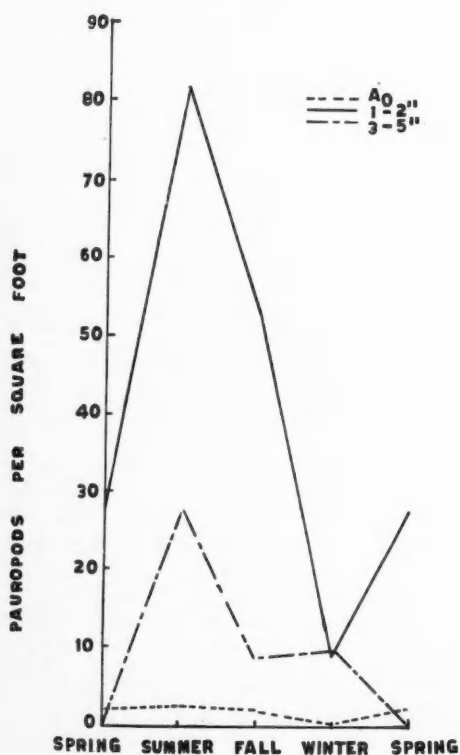
14

FIG. 14. Numbers of pauropods collected in relation to the moisture percentage of the oven-dry weight of the  $\frac{1}{2}$  in. and  $\frac{3}{5}$  in. depth of sandy soil.



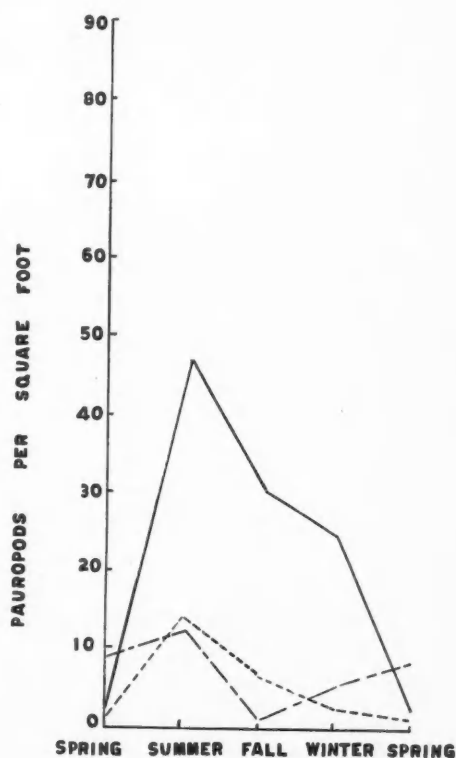
15

FIG. 15. Numbers of pauropods collected in relation to the moisture percentage of the oven-dry weight of the  $\frac{1}{2}$  in. and  $\frac{3}{5}$  in. depth of the clay soil.



16

FIG. 16. Numbers of pauropods collected from pine stands on sandy soil in relation to the seasons (spring, March 15-June 15; summer, June 15-September 15; fall, September 15-December 15; winter, December 15-March 15).



17

FIG. 17. Numbers of pauropods collected from oak stands on clay soil in relation to the seasons.



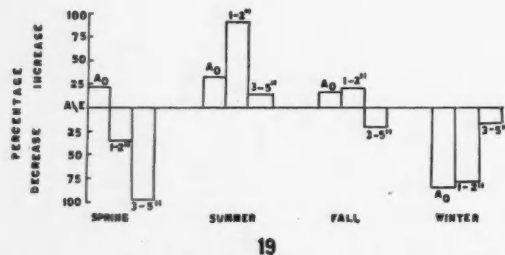
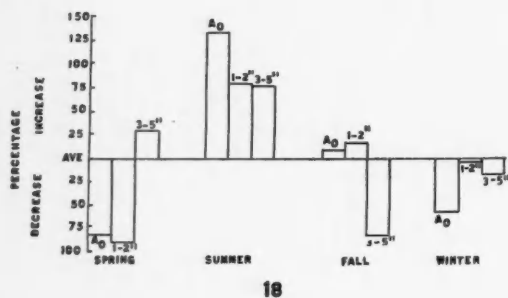


FIG. 18. Percentage of increase and decrease of numbers of pauropods collected from pine stands on sandy soil in relation to the seasons.

FIG. 19. Percentage of increase and decrease of numbers of pauropods collected from oak stands on clay soil in relation to the seasons.

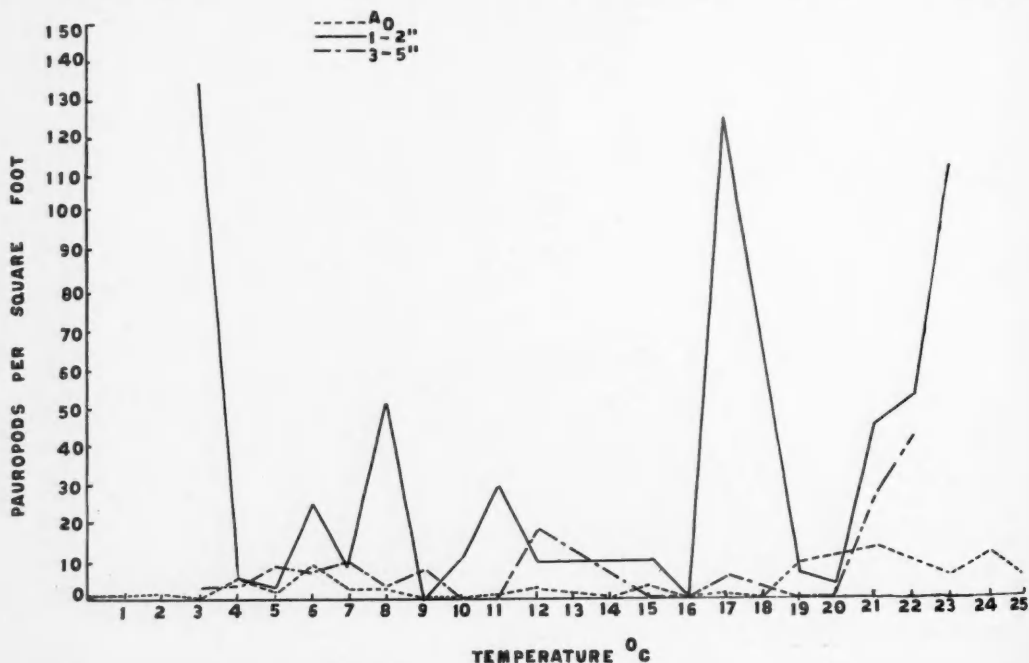


FIG. 20. Numbers of pauropods collected in both soil types in relation to the temperature of the A<sub>0</sub> Horizon, 1/2 in. depth, and 3/5 in. depth.

Figure 19 gives comparatively the same correlations between seasons and pauropod populations in the clay loam of the oak stand.

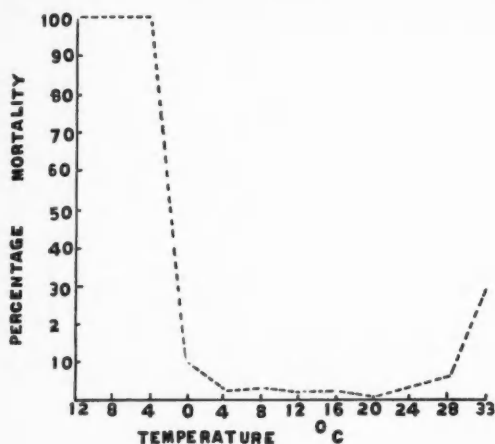
There appeared to exist a correlation between soil temperature and density of population, which is substantiated by the temperature experiments conducted in the laboratory. Figure 20 shows that, excepting in the one instance at 4° C. when the number exceeded all others and no doubt was unusual, the greatest number of animals was collected from all depths when the temperature range was between 17 and 24° C. The graph also shows that pauropods existed in the field at temperatures as low as 2° C., but in reduced numbers.

The pH in both soil types at the levels tested ranged between 5 and 6.

#### TEMPERATURE TOLERATIONS

In a study made of the mortality rate of pauropods at various temperatures, the rate was calculated from the numbers of animals (the greater portion of which was *Pauropus carolinensis*) added to the cultures for any particular temperature. Figure 21 shows the results obtained. The death rate appears to be low at temperatures between 4 and 24° C. A sharp increase is observed after these temperatures have been exceeded.

At 33° C., activity almost ceased, only slight movements were detectable even when an animal was



## 21

FIG. 21. Percentage of mortality (based on the average number of animals added per day) in relation to constant temperatures.

stimulated. At 0° C., animals that have been kept at room temperature died within twenty-four to forty-eight hours. If, however, animals which had been kept at 4° C. were exposed to 0° C. they in some cases lived as long as seven or eight days, but were completely inactive. Below 0° C. all animals died within two to three hours. At 8-12° C. the bodies of animals tested appeared to be "telescoped" but some individuals moved quite often on their own initiative. At colder temperatures (0-4° C.), however, the telescoping was not observed, the animals appeared to be well extended but quite inactive. If optimum temperature can be based on activity and low mortality rate, the data from the writer's experiments suggest that it is 16-20° C. This optimum temperature is comparable to that of Michelbacher (1938) suggested for a garden centipede.

## LIFE HISTORY OF PAUROPUS CAROLINENSIS

The funnel method of collection afforded the writer an opportunity to obtain various instars known to exist among Pauropoda. In the case of *P. carolinensis*, eggs and all post embryonic stages were studied. Instars of *Eurypauropus spinosus* with three, five, six, eight, and nine pairs of legs were observed, but no eggs were obtained. In the case of *Brachypauropus pearsei* only specimens with five and six pairs of legs were collected. Careful searching will no doubt furnish a complete life history of each of the species mentioned. The following description gives the life history of *Pauropus carolinensis*, the largest and apparently the most numerous species in the Duke Forest.

## Eggs.

Eggs were laid in groups of from three to twelve while the females were captive in the rearing dishes

during the months of June and July. Previous records (Harrison 1914) indicate that for *Pauropus amicus* the eggs were laid in groups of twelve to twenty, each egg being "perfectly spherical, pearly white, and 0.17 mm. in diameter . . . the outer membrane, which is opaque, appeared covered with minute pustulations." This description might well suffice for the physical appearance of the eggs of *Pauropus carolinensis*.

On the twelfth day, the outer membrane of the egg breaks. The embryo partially emerges, its anterior end becomes free, while the posterior end is still enclosed in the membrane. The embryo is covered by an embryonic membrane, which bears outgrowths that cover the antennae. The three pairs of legs are visible inside. The embryo remains motionless in this condition for three days; and then by a dorsal splitting of the second cuticle, issues out as an actively moving hexapod larva (Harrison 1914). Unfortunately, the present investigator was unable to observe this hatching process in *Pauropus carolinensis*, but assumes that the incubation period and process of hatching is comparable to that of Harrison's species. Numbers of "hexapod larvae," however, were collected and the post-embryonic development, which is anamorphic, was recorded and summarized.

## First Instar.

The six-legged pauropod has three dorsal tergites which are conveniently indicated as A, B, and F, tergite F being the definitive sixth tergite. It appears that the animal is composed of five postcephalic somites with an additional pygidium. Somite one bears a pair of rudimentary legs; functional leg-pairs are located on the preceding three somites. Tergite A partially covers, somite one and entirely covers somite two. Tergite B covers two and three, and tergite F the legless (definitive eleventh) somite. The tactile setae are two in number, the first extending from the anterior corner of tergite B, and the second extending backwards from the posterior corner of tergite F.

## Second Instar.

The animal issues from the old exo-skeleton with an additional tergite (C). This tergite is interpolated between the last two of the previous stages and covers two additional somites which bear legs. Leg pairs one, four, and five are with five segments; the intermediate pairs consist of six segments. The coxa and trochanter of legs four and five bear biramous setae; all the others bear simple setae. Situated toward the middle and one on each side is an additional pair of tactile setae. As in the preceding instar, tergites A and B cover two somites each; the last tergite covers only one somite and which is without appendages. The antenna has three basal segments. The animal ranged in length from 0.6 mm. to 0.7 mm.

*Third Instar.*

After a second molt the larvae have five tergites. The new one covers two additional somites, only the more anterior of which bears a pair of appendages. Nine postcephalic somites including the pygidium are evident. The first bears the rudimentary legs, the second, third, fourth, and fifth somites each bears a pair of legs. The last two somites are legless. Leg pairs one and six are composed of five segments each; intermediate legs have six segments. Only the coxa and trochanter of the sixth pair of legs possess biramous setae. There are four pairs of tactile setae—the first, second, and fourth, as in the last stage. The third pair projects posteriorly from a little behind the middle of the fourth tergite. The basal portion of the antennae consists of three segments. The average length of the animals of this stage, based on measurements of five well-extended specimens, is 0.92 mm.

*Fourth Instar.*

References indicate that it was once believed that when a pauropod molted its third time it issued with fourteen legs. Lubbock (1866) says "as I have met with many specimens possessing, respectively, seven pairs and eight pairs, we may, I think, safely conclude that a new pair is added at each molt after the first until the full number is acquired." Kenyon (1895) states "In the next stage there are seven pairs of legs, and probably four pairs of lateral hairs, five dorsal plates, and nine body segments, judging from what happens in the five-leg stage. The facts in the case I have not had the opportunity to learn." Harrison (1914) believed that since he had found numerous specimens of all other stages except the seven leg-pair, such a stage did not exist. He had hoped by observing a twelve-legged specimen molt "to prove definitely that no stage with fourteen legs occurred. But although it molted successfully, it was, unfortunately, so badly crushed between two pieces of bark in removing it from the tube that the number of legs could not be made out." Hilton (1929) discussed specimens having three, five, and six pairs of legs, and although he never found specimens with seven or eight pairs of legs, suggested that his intermediate forms "confirm Lubbock's observation and help to confirm his conclusions that the stages in *Pauropus* are first a six leg, next a ten legged form, then a twelve, then a fourteen, then a sixteen, and finally the eighteen legged form of the adult."

The writer was fortunate in that he was able to observe an animal with sixteen legs issue from a molted skin that had only twelve legs. This leaves no doubt that in the case of *Pauropus carolinensis*, and probably in most other Pauropoda, two pairs of legs are added on the third molt.

The first of the new leg pairs appears to belong to the legless somite (eighth) of the previous stage, the second to the new somite interpolated between the last two terga. In all, ten postcephalic somites

are evident, two beneath each of the first three terga, two and part of the ninth underlie the fourth tergite. The remainder of the ninth and tenth somite are beneath the last tergite. All somites except the first and tenth bear a pair of appendages. Leg pairs one, seven, and eight are 5-segmented, the intermediate pairs have six segments. The coxa and trochanter of the seventh and eighth pair of legs each possesses a biramous seta, those of the sixth pair are now simple. In the male two penes appear to be situated at the base of the second pair of legs. The body has increased to 1.18 mm. in length. The basal portions of the antennae consist of four segments, which is the adult number. As in the previous stages, the dorsal and anal setae are similar in arrangement to those of the adult. The anal plate has increased in size with each succeeding instar and appears to have reached the adult size in this stage. The rami and flagella have also reached the adult proportion.

*Adult.*

On the fourth molt animals emerge as adult forms. A new tergite (E) is formed between the last two of the previous stage and covers the ninth and tenth somites. The tenth somite is newly formed and bears a pair of legs which along with the first pair are 5-segmented; all others possess six segments. Only the ninth pair of legs has coxa and trochanter with biramous setae. The additional tergite bears a pair of tactile setae situated towards its posterior margin, and each seta extends backwards.

Table 8 summarizes the life history of *Pauropus carolinensis*.

## MOLTING

An animal with a rigid exo-skeleton must, in order to grow, shed its outer covering along with its "chitinous intima." During such a complicated process, organs are being reconstructed and even new structures formed. Such conditions may render an animal helpless and motionless for a time (Verhoeff 1928, 1937).

Among Pauropoda, the length of time that elapses between molts has not been recorded. Lubbock (1866), however, was able to keep alive a six-legged specimen of *Pauropus huxleyi* from October 24 to December 6 of the same year (at which time it died) without molting. Specimens of *Pauropus carolinensis* molted as early as four days after being collected. Whereas, others of the same age and collected at the same time remained four months without any change. Obviously, laboratory conditions were not conducive to molting and pauropods that did molt had undergone preparatory stages of molting before being captured.

*Pauropus carolinensis* was observed to molt several times and in all cases the time for shedding the skin was very short, about 25 minutes. Before passing into a molt, the pauropod became rather inactive. The body took on a rigid appearance, but remained in an upright position throughout the process. The antennae along with the head were bent ventrad. As

TABLE 8. Number of tergites, number of postcephalic somites, number of leg pairs, location of tactile setae, and mean length of individuals of each stadium in the life history of *Pauropus carolinensis*.

STADIUM	TERGITE		SOMITE postcephalic		LEG PAIR		TACTILE SETAE		LENGTH
	No.	Tergite	No.	Somite	No.	Leg Pair	No.	Seta	
I	3	A	5	1	3	0	2	0	?
				2		1			
		B		3		2		1	
				4		3			
II	4	A	7	1	5	0	3	0	0.67mm (Ave. of 2 speci- mens).
				2		1			
		B		3		2		1	
				4		3			
III	5	A	9	5	6	4	4	2	0.92mm (Ave. of 5 speci- mens).
				6		5			
		C		7		6		3	
				8		0			
IV	5	A	10	1	8	0	4	0	1.18 mm (Ave. of 10 speci- mens).
				2		1			
		B		3		2		1	
				4		3			
V	6	A	11	5	9	4	5	2	1.5 mm (Ave. of 10 speci- mens).
				6		5			
		B		7		6		3	
				8		7			
ADULT	6	A	11	9	9	8	5	4	
				10		9			
		B		11		0		5	

the molting continued the animal first freed its head and by forward propulsions started to work its way out of the skin. Finally the antennae were freed and the pauropod gradually emerged. When shedding

was almost complete the propulsions were more vigorous and in time the animal was seen moving forward slowly dragging the old skin. Finally, the white, moist, and weak animal was entirely freed.

The total number of molts for *Pauropus carolinensis* is four.

## DISCUSSION

Since 1866, when Lubbock first noticed and described *Pauropus huxleyi* and designated Pauropoda as an order of Myriapoda, at least one hundred and twenty other species have been described. The present paper records six from Duke Forest. The members of the group are now generally recognized as primitive arthropods and Pauropoda constitute one of the four distinct classes of "myriapods." At the present six families of Pauropoda (Asphaeridiopodidae, Brachypauropodidae, Eurypauropodidae, Pauropodidae, Polypauropodidae, Scleropauropodidae) are known to occur. At least three of these (Brachypauropodidae, Eurypauropodidae, Pauropodidae) are represented in Duke Forest. The writer reports Brachypauropodidae from North America for the first time and extends the geographical range of Eurypauropodidae southward to North Carolina.

Authorities believe pauropods to be rather generally distributed with exception of the arctic, antarctic, and desert regions. Wherever found, they inhabit dark, slightly damp niches; under decaying logs, under stones and lumps of clay (Hansen 1902, Hilton 1928, 1930), among leaf litter and in the soil itself.

In contrast to most other myriapods, pauropods are delicate and fragile creatures with thin, chitinous exo-skeletons, unable to withstand exposure for any length of time. They are rather definitely confined to humus layers in forests. Little or nothing has been known concerning the comparative numbers of pauropods with respect to other myriapods. Of all the myriapods collected during the writer's work, 40.8 percent were pauropods. Annual average estimates of pauropods per acre for sandy and clay soil are 2,178,000 and 1,672,704, respectively. The numbers of pauropods present in the soil in some degree indicate their importance as constituents of the habitats they occupy.

The realization of the part played by animal life in soil formation has been gradually growing for the last fifty years. The forest soil must be subjected to some sort of mechanical cultivation so that it may be kept friable and porous for plant growth and also so that organic residue may be decomposed. Cultivation of forest soils is accomplished by soil animals, but they do not confine their work to this. They decompose leaves and branches, bite them into bits, let the organic material pass through their intestinal canals, and thus make it more accessible to the bacteria and fungi which carry on the final processes of humus formation (Bornebush 1930). Although pauropods are one of many groups of soil animals, the striking high incidence of pauropod population would

lead one to believe that regardless of the small size of the animals, their role in soil formation is significant.

The vertebrate animals, the larger insects, the earthworms, the Protozoa, and to a certain extent the nematodes of the soil have been studied and their effect observed. The microarthropods, comprising the pauropods, scolopendrellids, proturans, collembolans and free living mites have been entirely overlooked, probably on account of their size, and to the need of special methods to find them (Jacot 1936). This paper opens a field of investigation concerning the neglected microarthropods and present information that should be of great importance in determining the role pauropods play in the soil.

Pauropods range in length from 0.5 mm. to 1.8 mm. Their small size has made it unusually difficult for one to collect and study them. The funnel method of collection as used in this investigation proved to be satisfactory in securing large numbers. The method is based chiefly on the fact that pauropods are particularly sensitive to desiccation and move downward with increasing dryness.

There is a law of nature that increase in numbers is directly proportional to the availability of food and protection. Different cover and soil types vary in their ability to furnish these two requirements. It seems necessary, therefore, to know the physical conditions of soil in order to attempt to understand the many interesting factors that have to do with the distribution of animals of soil.

Sand is dry and loose, caves readily, and has a variable temperature. Clay is cold, dense, poorly aerated, and tenaciously holds moisture but when dry is dense and hard (Pearse 1939). It is evident that soils differ considerably in their capacity for water retention. Thus a heavy clay soil with 15 percent moisture might be apparently dry, while a sandy soil with the same amount of moisture would be visibly moist (Robinson 1936). Soil profiles indicate the constituent layers and their respective thickness. In sandy soils the humus layer is usually thin, as a great deal of the organic material has filtered to the A<sub>1</sub> horizon. Comparatively little organic material is found beneath the thicker humus layer in most clay soils, since particles of soil are more compact and prevent filtering to a great extent.

With such facts as these in mind, the writer's data may be interpreted. Since there has been no other work of an ecological nature on Pauropoda, the present comparison of data must be based in part on results with various other closely allied animal groups.

The movement of microarthropods in soil is regulated chiefly by moisture. Cook & Loomis (1928) state that "the outstanding requirement for the existence of delicate humus animals is a continuous supply of moisture, not necessarily a regular supply, but one that is never completely interrupted or the creatures at that place are exterminated." It has been shown that moisture is a significant factor in

the distribution of pauropods. In both sandy and clay soils a greater number of pauropods was found at all levels where optimum percentage of moisture was determined (Figs. 14, 15). However, in clay soil optimum moisture percentage, based on the greatest numbers of pauropods present, was higher than in sandy soil. As sandy soils differ from clay soils in moisture content, one may expect the population to be differently distributed.

During periods of drought minute animals, such as pauropods, have an advantage over larger animals in that they are able to crawl through cracks and crevices to take advantage of any moisture that may be present, even at considerable depths. A dry surface should not endanger the existence of any humus feeders, for the animals can seek refuge in moist subsoil, if the nature of the soil permits.

More pauropods were found in the 1-2 in. and 3-5 in. levels in the clay soil than in the sandy soil during summer, when the writer's records show that more moisture was present in the clay. However, clay soils usually have little in the way of humus fauna. When small soil animals do exist in colloid soils, they are found in the "humus blanket except as the character of the soil may be modified under this blanket" (Cook & Loomis 1928).

Pauropods were found by the writer to occur most often in sandy soil of pine stands (Figs. 12, 13), although twenty-eight per square foot were found in clay soil. In the thicker humus of oak stands beneath which was a clay soil, the number of pauropods exceeded those in the same layer of pine stands on sandy soil by five times. The physical nature of soil possibly accounts for the greater density of population at the 3-5 in. level in sandy soil.

Temperature no doubt plays its part in the general distribution of pauropods, which have been collected from areas 65° N. to 34° S., from sea level to altitude of 2,000 meters (Hilton 1931, Hansen 1902). Single species do not appear to have a wide geographical range. As to their vertical distribution in the soil, the present work suggests that to gain thermal stability of the soil, pauropods seek lower levels during the winter when the air temperatures are extreme (Figs. 16, 17). High temperatures produce a torpid and inactive state among pauropods. In the summer and fall, for protection against heat and desiccation, especially in sandy soils, these animals migrate to the A<sub>1</sub> horizon where conditions are cooler and more moist. In constant temperature cabinets, as well as in field soil, optimum temperature was found to be between 16 and 20° C. Michelbacher (1938) found the optimum temperature for a garden centipede (*Scutigera immaculata*) to be between 12 and 20° C. The writer has shown that at least one of the foods of *Pauropus carolinensis* is fungi. Dr. F. A. Wolf of the Botany Department of Duke University has suggested that in general, the optimum temperature for molds is between 10 and 30° C. Since the optimum temperature for pauropods falls within that for mold growth, there appears to be a



correlation between the incidence of pauropod population and that of mold fungi. Specialized food habits are indicated by the minute mouth parts of Pauropoda.

Their locomotion has been described as being of a fast or slow type. Some observers (Latzel 1884) believed the former indicated carnivorous habits. Harrison (1914) believed Pauropus (a fast type, according to Latzel) to be a humus feeder. But on what part of the humus does it feed? The H layer of the A<sub>1</sub> horizon is composed of brown, brownish black, or black amorphous organic matter. It seems quite possible then if pauropods should feed off dark organic matter, their gut (which is visible through the chitinous exterior) would appear dark also. This was not the case in any instance. As has been mentioned, the writer observed *Pauropus carolinensis* feeding only on mold fungi and since the optimum temperature for growth of molds may be also that for the greatest numbers of pauropods, it seems possible that the pauropods would have access to enormous amounts of food.

Harrison (1914) collected eggs of *Pauropus amicus* and the writer, eggs of *P. carolinensis* during the months of June and July. A decided increase in numbers of pauropods was noted in A<sub>1</sub> horizon in the late spring of 1941 and considerable numbers continued to occur through the summer (Figs. 16, 17). Optimum conditions of temperature, moisture, and food supply exist at such times. During the fall, when moisture percentage decreased, the numbers of pauropods decreased. As winter approached the animals no doubt traveled to lower levels to seek the thermal stability, but many died during such migration.

### SUMMARY

1. During 1940-42 three families of Pauropoda, represented by six species, were collected from the Duke Forest. The species represented were: *Brachypauropus pearsei* Starling; *Eurypauropus spinosus* Ryder, 1879; *Pauropus carolinensis* Starling; *Pauropus causeyae* Starling; *Pauropus dukensis* Starling; and *Stylopauropus* sp. Starling. These were the first species of pauropods reported from the Southeastern United States, and the first instance of *Brachypauropus* being collected in North America.

2. Eight new species of Chilopoda, and one or possibly two new species of Symphyla were collected during this investigation. Four species (three Chilopoda and one Symphyla) not heretofore found in North Carolina were reported, making a total of one hundred and eighteen species of 'myriapods' which have been described from North Carolina.

3. Of the 1,796 myriapods collected through funnels, 40.8 percent were Pauropoda, the most numerous of any group of "myriapods."

4. Quantitatively, the distribution of pauropods in the soil may be effected by cover type and structure of the soil.

5. A calculated estimate shows an annual average of 1,672,704 pauropods per acre (to a depth of 5 inches) in oak stands on clay soil, as compared to 2,178,000 in pine stands on sandy loam.

6. Thirty-seven pauropods per square foot were calculated in the 1-2 in. layer of sandy soil; while only twenty-eight per square foot were collected from clay.

7. Five times as many pauropods were found in oak humus on clay soil than in the same level under pine stands on sandy soil.

8. Twelve pauropods per square foot were found in the 3-5 in. samples in the sandy soil, as compared to five per square foot in clay soil.

9. Moisture and temperature are two factors that may affect the distribution of pauropods.

10. The greatest number of pauropods was collected from each level in sandy soil when the moisture percentage of the oven-dry weight was 11-20. In clay soil pauropods appeared to prefer 21-30 percent of moisture at both levels.

11. Summer appeared to be the most favorable season for the development and activity of pauropods. Eggs were obtained in June and July. During the winter the percentage of decrease in numbers was found to be least in the 3-5 in. level.

12. The optimum range of temperature based on activity and mortality rate, when pauropods were placed in constant temperature cabinets, was found to be 16-20° C.

13. The optimum temperature, based on field observations relative to number of pauropods present in the soil samples, was found to be 17-23° C.

14. A correlation appears to exist between optimum temperature for mold growth in general and high incidence of pauropod population. Mold fungi were observed to be the usual food of *Pauropus carolinensis*.

15. The number of pauropods per acre of forest soil indicate to some degree their economic importance. Along with the numerous other animals of the same habitat they render the soil friable and porous for plant growth and aid in the decomposition of organic materials.

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SOME ASPECTS OF THE ECOLOGY OF THE  
IGUANID GENUS UMA

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## SOME ASPECTS OF THE ECOLOGY OF THE IGUANID GENUS *UMA*

### INTRODUCTION

The lizards of the genus *Uma* are known colloquially as fringe-footed or ocellated sand lizards. The former designation has resulted from the presence on certain of the digits of elongate, pointed scales forming fringes along the sides of these structures (Figs. 18 and 19). The latter refers to the dorsal pattern of eye-like maculae (Fig. 1). The body, including the tail, is conspicuously depressed. The skin exhibits a fine granular scalation. The festooned toes, flattened body and smooth skin are morphological features associated with the sand burrowing habit of these reptiles.

The members of the genus occur in aeolian accumulations in southwestern United States and parts of northern Mexico. Distribution is discontinuous throughout the range since the animals are restricted to deposits of fine loose sand. In such places they seek cover by the so-called "sand-swimming" behavior. Sand-swimming implies submergence into the loose substratum of the habitat by diving or wriggling into the soil rather than by construction of a burrow or tunnel for retreat. Fossorial activity of this type results in direct contact between the surface of the animal's body and the small fragments which compose the wind-blown deposits.

The habitat presents rigorous environmental conditions. The configuration of the substratum is being modified continually by wind action; transportation and deposition of sand is going on almost incessantly. The habitat is one of pronounced aridity with few plants growing on the dry, shifting soils. Temperature fluctuations are extreme. These and other factors combine in the formation of an en-

vironment which, inhospitable to life, places great stress upon adaptive modifications.

The lizards are highly specialized, possessing numerous structural and functional adaptations associated with the arenicolous habit. The primary purpose of the present study has been to interpret such structures and their functioning in terms of the environment.

Before entering into a discussion of the ecology of the genus, it is important to draw attention to recent changes in nomenclature. Heifetz (1940) has published a review of the lizards of the genus *Uma* in which he designates three species and one subspecies. Previously to this work, the single species, *Uma notata* was recognized. Changes in taxonomy which antedate this classification may be obtained from this paper.

The three species and one subspecies as now recognized are *Uma scoparia* (Mojave Desert of California), *U. inornata* (Coachella Valley of the Colorado Desert of California), *U. notata notata* (Colorado Desert south of the Salton Sea, California), and the subspecies *U. notata cowlesi* (Northwest coast of Sonora, Mexico).

The remarks made in the succeeding pages apply with equal weight to all known members of the genus unless otherwise specified.

### HABITAT

The habitat occupied by *Uma* characteristically exhibits unstable edaphic conditions. Few plants are able to withstand the inhospitable rigors of aridity coupled with a shifting substratum. The paucity of vegetation and the difficulty of burrow maintenance in the superficial layers of sand, except dur-

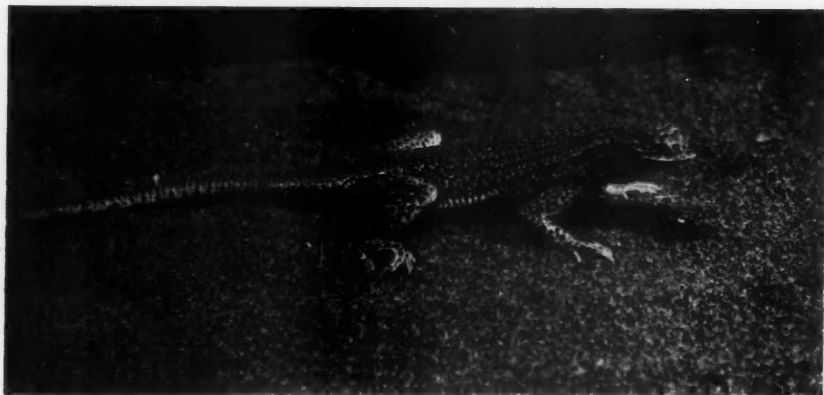


FIG. 1. An adult fringe-footed sand lizard (*Uma inornata*) from the Garnet aeolian deposit in the Coachella Valley, California. (Photo by R. B. Cowles.)



ing brief periods following rains, are environmental features which have contributed to the extensive adoption of the sand-swimming habit.

Sand submergence not only is a method of escape from enemies, but also is a means of retreat from undesirable temperatures. The sand, with its numerous air spaces, serves as an insulating blanket, protecting the reptiles from adverse fluctuations. Within certain limits of the temperature range, optimum conditions may be approached by adjusting the depth of burial.

#### NATURE OF THE SAND

The most consistent general feature of the areas occupied by the genus is the presence of sand of a texture which facilitates subsurface retreat for juvenals as well as adults. Such substratum requirements are most frequently met by aeolian deposits. Sand accumulations resulting from the action of water, such as those which occur in washes and flood plains, though often exhibiting sand of suitable texture, are subject to sporadic inundation and thus such regions are untenable. Further, such deposits frequently exhibit cementing of the sand grains which interferes with or completely prevents sand-swimming. I know of no cases of occurrence of the animals in such deposits.

Measurement of sand particles from a preferred sector in the Garnet habitat, 5 miles north of Thousand Palms in the Coachella Valley, showed a surprising consistency in size. Approximately three fourths of the fragments in each sample were slightly less than 0.5 mm. in diameter. The remainder were under 1 mm., with the exception of a small percentage, perhaps 0.01 percent, which were over 1 but under 2 mm. in size. Larger particles were not found in this particular sector.

Comparison of sand from other habitats frequented by the genus with that of the selected portions of the Garnet deposit suggests that sand composed of particles greater than 2 mm. in diameter is generally avoided. Captive specimens submerged more frequently in the finer soil from the Garnet area than in coarser material with a particle size approximating 2 mm. Nevertheless, the occasional behavior of specimens in the laboratory suggests that burrowing in nature may sometimes occur in such deposits, but it is unquestionably rare. The cumulative experience of many collectors and the personal observations of the writer have led to the conclusion that coarse deposits are consistently shunned. Such sand offers mechanical resistance to sand-swimming. Captive adult animals are noticeably retarded in speed of submergence in coarse sand (i.e., sand with the majority of particles over 2 mm. in size). Juvenals are unable to enter such material without great expenditure of energy. Frequently they become exhausted and are satisfied with only partial burial. The disastrous effect of such retardation under natural conditions, where speed of sand-swimming is essential for escape from predators, is readily apparent.

#### PLANTS OF THE HABITAT

The continually shifting sand supports a meager plant community throughout most of the year (Figs. 2, 3). Where it is of considerable depth and constantly moving before prevailing winds, such as is the case with the crests of barchanes and dunes, conditions of growth are especially severe. However, about the periphery of such motile deposits the soil may be sufficiently stable to permit a sparse growth.

In the spring, throughout most of the range of the genus, numerous annuals appear which, though transitory types, provide both food and cover for the lizards. A number of factors contribute to the development of this short-lived rather profuse growth. Among them are vernal decline in wind velocity, silting from sporadic rains, and the inherent capacity of the plants for ecesis on the loose soil.

#### ARIDITY

The habitat is one of extreme dryness. Water, usually in the form of rain or dew, occurs only a few times in a year. The animals therefore must depend essentially upon water derived from their arthropod and plant foods.

#### VARIATIONS IN THE HABITAT

The statements made thus far relate to the general features of the habit considered in its broadest sense. There yet remains to be considered certain of the more conspicuous differences which exist between the various regions occupied by *Uma*—such as sand color, plant species, and the topography of the deposits. Certain illustrative areas in California and Sonora, Mexico, have been selected—the Garnet area, the Coachella dunes, the Salton Sea Sandy Beach accumulation, and the Yuma and Rice regions. The Garnet deposit, serving as a typical habitat, has been chosen for a somewhat more detailed analysis than the other sectors.

#### THE GARNET DEPOSIT

Details of topography and to a considerable extent the occurrence of plants in an aeolian deposit vary from year to year. The description to follow of the Garnet habitat is as of spring, 1942.

This deposit is located a few miles north of Thousand Palms in the Coachella Valley (Fig. 2). The accumulation of wind-blown sand is situated in a small depression located on the east side of the Coachella Valley at the base of the Little San Bernardino Mountains. A low hill lies between the deposit and the level country to the west. The valley in which the accumulation occurs opens toward the south.

The sand, whitish in color, is deepest (at this writing) on the west side of the habitat. Here in some places it may assume dune proportions, heaping up to a height of 4 or 5 feet. Vegetation is absent in this region. Not far from the deeper sand, along its eastern margin, are found numerous hillocks



FIG. 2. The Garnet deposit, located north of Thousand Palms in the Coachella Valley. This sand accumulation is occupied by *Uma inornata*. (Photo by R. B. Cowles.)

topped most frequently by Creosote Bush (*Larrea divaricata* var.) and less commonly by Desert Mint (*Hyptis Emoryi*) while many of the smaller hummocks are crowned by Burro Weed (*Franseria dumosa*). Sand has accumulated about these plants and other impediments to form heaps which in many places are 2 or 3 meters high. The hillocks are characteristically elliptical in shape with their long axes lying in the direction of the prevailing winds with the bush or other obstruction responsible for the deposition of the sand situated at the windward end. Between the vegetation-free dune sand and the creosote-topped hummocks, occurs a rather profuse growth of the annual, *Dicoria canescens*. This rather dense growth attracts many lizards by providing food and cover. The sand in this *Dicoria* belt is fine and loose for a considerable depth.

Sand in the Garnet area varies as to particle size and depth of accumulation. Variation in wind velocity throughout the habitat has resulted in the deposition of grains graded as to size. In a few places coarse sand averaging 2 mm. in diameter predominates; in others, more extensive in occurrence, the majority of particles may approximate 1 mm. in diameter. Most of the sand in the dune area and on the lee side of the hummocks is extremely fine, measuring, on the average, under 0.5 mm.

In contrast to the abundant loose material in the dune region and about many of the hillocks, the sand occurring in the unobstructed troughs between these elevations may be only 1 to 3 cm. in depth. This thin layer often lies upon a compacted stratum which has been produced largely by the deposition of finer particles washed into the hollows from adjacent hummocks by sporadic rains.

#### OTHER AREAS

In general, all other regions occupied by the genus conform to the analysis of the Garnet habitat. Salient features in which certain other well-populated sectors depart from the general conformity may be briefly stated:

*Coachella dunes.* Located near Indian Wells, south-east of Palm Springs—occupied by *Uma inornata*.

Salt Bush (*Atriplex* sp.) is more frequently found crowning the small hummocks. Mesquite (*Prosopis chinensis*) is conspicuously associated with the giant dunes near Indian Wells. The sand color is similar to that in the Garnet area.

*Sandy Beach.* Situated on the west side of the Salton Sea—occupied by *Uma notata notata*.

Numerous barchanes almost devoid of vegetation are common in this region. Plants which cling to the margins of the windward side of the dunes are chiefly Buckwheat (*Eriogonum* sp.). Sand color is buffy or reddish brown.

*Yuma dunes* (Fig. 3). Located in the southeastern part of the Imperial Valley, extending over into Sonora, Mexico—occupied by *Uma notata notata*.



FIG. 3. Sparsely vegetated dunes of the Yuma, Arizona region occupied by *Uma notata notata*. The plants in the foreground are Desert Willow, *Chilopsis linearis*. (Photo by R. B. Cowles.)

The Yuma region is characterized by its vast extent of dunes covering many square miles—much greater than any of the other areas discussed. The dominant vegetation is Desert Willow (*Chilopsis linearis*) and Palo Verde (*Cercidium Torreyanum*). Creosote Bush (*Larrea divaricata* var.) is less abundant here than in other sectors.

*Rice deposit.* Located in southeastern part of the Mojave Desert—occupied by *Uma scoparia*.

Many clumps of vegetation with numerous small intervening spaces of exposed sand occur in this sector. The most conspicuous plants are Galleta Grass (*Hilaria rigida*) and short Creosote Bush. There are no prominent dunes.

#### ADAPTATIONS FOR ARENICOLOUS LIFE

In common with lizards of other genera such as *Mabuia*, *Ptenopus*, *Teratoscincus*, *Phrynocephalus*, and *Callisaurus*, which live in similar habitats throughout the world, numerous sand adaptations occur in *Uma*. Certain of the more conspicuous of these adaptations as found in *Uma* are as follows:

## Adaptations connected with:

1. Locomotion upon and beneath loose soil.
  - a. Increase in foot surface by extension of length and breadth of the toes facilitates support and propulsion.
  - b. Predominantly granular smooth sealation minimizes friction during sand-swimming.
  - c. Depressed body form and shovel-shaped head facilitate submergence by lateral movements of the anterior portion of the body.
2. Respiration beneath the sand.
  - a. Location of external nares and presence of nasal valves both tend to prevent inhalation of sand fragments.
  - b. Configuration and function of nasal channels facilitates the exclusion and ejection of sand grains.
3. Protection of the sense organs, especially the eyes, ears and olfactory apparatus.
  - a. Eyes
    - (1) Overlapping eyelids tend to prevent the entrance of sand and evaporation of water from the orbital region.
    - (2) The nictitating membrane functions in the removal of accumulated sand.
  - b. Ears
 

Ear-flaps protect the tympanic membranes from the abrasive effect of wind-blown sand and particles encountered in sand-swimming.
  - c. Olfactory apparatus
 

Nasal valves tend to occlude external nares. (See No. 2.)
4. Occlusion of sand from body openings.
  - a. A counter-sunk lower jaw prevents the oral acquisition of particles during sand-swimming.
  - b. Nasal valves tend to block the external nares.
  - c. Ear valves occlude the external auditory meatuses.
5. Concealment.
  - a. The dorsal color pattern resembles the sand of the habitat.
  - b. The depressed body form presents a low silhouette.
  - c. Cast shadow is concealed by squatting close to the substratum.
  - d. Sand-swimming facilitates escape from enemies and undesirable temperatures.

The adaptations mentioned do not constitute a complete picture of the structural and functional modifications which appear in the genus *Uma*. Rather, they represent those which by their conspicuousness either have been discussed already in the literature or have been studied by the author.

In the succeeding pages the following subjects are discussed: Vision and eyelids, the nictitating membrane, the olfactory apparatus, the parietal organ, hearing, locomotion, feeding habits, concealment, selection of places of retreat, enemies, and thermal tolerance.

Studies that have to do with the third eye or parietal organ constitute a large part of the following pages. Although this structure in modern *Lacertilia* has come to be generally accepted as being vestigial and in the majority of cases non-functional, in *Uma* the striking external appearance of the organ in conjunction with suggestive behavior led to its investigation.

## VISION AND EYELIDS

*Vision*

The eyesight of *Uma* is exceptionally well developed and may be accommodated effectively for distant as well as close vision. In the field, individuals watched through field glasses have been seen to capture very small rapidly flying insects, the movements of which were followed with difficulty by the observer. Similarly, on numerous occasions I have seen captive animals jump into the air to seize a fly or other small insect which flew within reach. The success of such behavior is dependent upon acute vision.

Likewise the animals see well at a distance, since I have startled individuals as much as 35 meters away. Part of the difficulty encountered in procuring specimens of this wary lizard is due to this excellent distant vision.

*Eyelids*

Adequate eye protection plays an important part in successful arenicolous life. Not only must the delicate eye surfaces be protected from the irritating and abrasive effect of sand particles which may be blown into the eyes, but the sand-swimming habit further jeopardizes these organs.

The eyelids of *Uma* are adapted for the exclusion of sand. Their over-lapping character and broad occluding surfaces, when firmly closed, effectively prevent most foreign material from reaching the eyes.

A conspicuous feature of the lids is the prominent festooning of their margins (Figs. 4, 5). The festoons fringe these organs completely. They possess no mechanism within themselves for movement but under certain conditions of eye closure such as during sand-swimming they may be forced together by the external pressure of sand or, when the lizards are on the surface, by the influx of blood and lymph into the eyelids. Bruner (1907) describes the structure and function of a distention mechanism in the head of certain of the *Reptilia*. This mechanism is well developed in the *Lacertilia*. By contraction of certain muscles, especially a ring of striated muscle fibers about the internal jugular veins, the blood pressure of the head is raised. Blood and lymph distend sinuses in the cephalic region, producing intumescence and swelling of the tissues. One function ascribed to the phenomenon is that of stretching and tearing of the cephalic skin facilitating exuviation of the head. Thus during periods of intumescence the

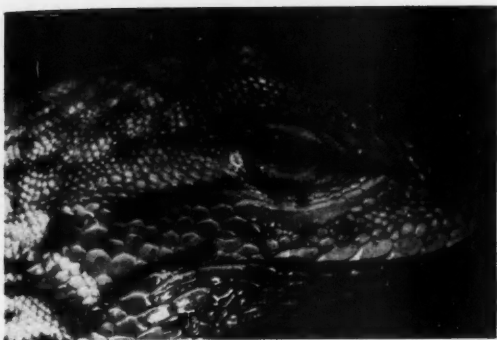


FIG. 4. Lateral view of the head of *Uma*. Note the broad festooned eyelids, the similarly festooned earflap (lower left hand corner) and the knife-like cutting edge of the upper jaw. (Photo by R. B. Cowles.)

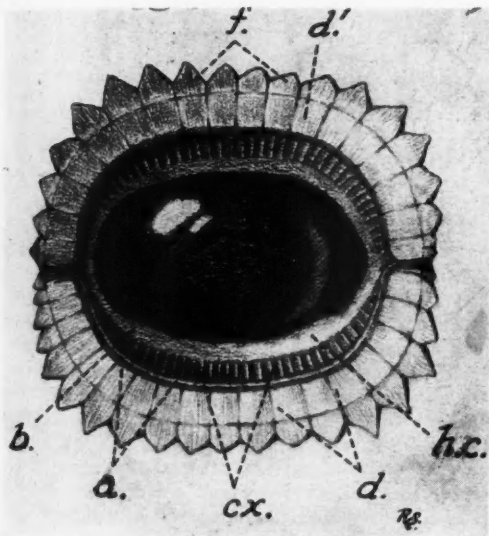


FIG. 5. Eye of *Uma* with the eyelids rolled back to expose their ocluding surfaces. (See Fig. 6 for explanation of abbreviations.)

fringing scales may be moved through changes in the turgidity of the underlying tissues.

The importance of the festoons may be twofold: (1) They increase the contacting surfaces of the lids, thereby rendering the occlusion of sand from the eyes more effective and (2) they may reduce the glare from the bright substratum of the habitat by intercepting and breaking up light reflected from the sand.

When the upper and lower lids come together, they usually meet along an inner and an outer ridge, both of which extend the length of the lid margin (Figs. 5, 6, a, b). A space may be left between these ocluding surfaces. The lining of this cavity is corrugated, the ridges and furrows extending transversely as shown in the illustration (Fig. 5, cx). The

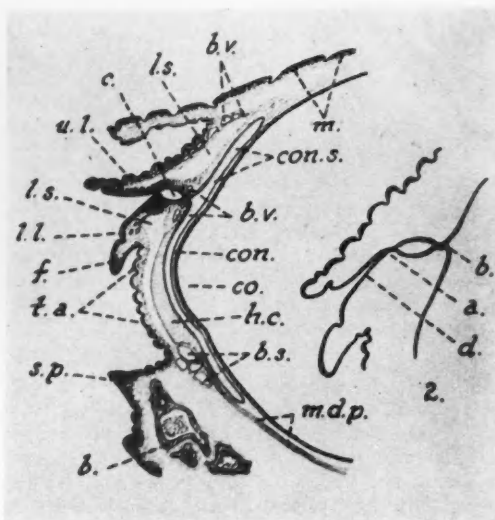


FIG. 6. Transverse section through the eye and lids of *Uma inornata*. a., outer ocluding ridge; b., inner ocluding surface; bo., bone; b.s., blood sinuses; b.v., blood vessels; c., chamber situated between inner and outer ocluding ridges; co., cornea; con., conjunctiva; con. s., conjunctival sac; cx., ridged and furrowed surface lying between the ocluding ridges, a. and b.; d. & d', surfaces which come into contact when the lids are tightly closed as during sand-swimming; f., festoon; h.c., hyaline cartilage; l.l., lower lid; l.s., lymph space; m., melanophores; m.d.p., palpebral depressor muscle; t.a., translucent area; u.l., upper lid.

significance of these corrugations is not clear although a certain amount of interlocking of these crests and valleys may occur when the lids are tightly closed, insuring effective closure of the organs.

The double occlusion of the lids is effective not only in preventing sand from reaching the delicate surfaces of the eye but also in minimizing evaporation of fluid from the conjunctival sac. If sand particles were to come into contact with the moist inner ocluding ridges, liquid would be drawn from the eye by capillary action. The additional contacting surfaces of the lids (Fig. 6, a) largely obstruct the entrance of such fragments and thereby are of importance in reducing the tendency for water loss by evaporation. Such evaporation would be of real consequence in an area where water is at a premium and the reptiles spend such a great part of their time buried in the dry sand.

The eyeballs, and thus the eyelids, may be projected outward by the contraction of certain muscles which lie ventral to the orbital blood sinus—a large part of which is situated beneath and behind the eye. The lizards often protrude the eyes rapidly upon coming to the surface. This is done before the eyes are opened. Its effect is to shake loose any sand grains which may be adhering to the skin of the eye region or that may have lodged between the free portion of the lids.



Although the overlapping eyelids are highly effective in excluding foreign matter, they do not wholly prevent the entrance of such material since wind-blown fragments may reach the eye surfaces. Sand pellets are frequently found in the anterior eye corners. The problem of the removal of this material will be considered later.

When the eyes are closed, the cornea rests against the lower lid; the lids meet dorsally to this region (Fig. 6). The lower eyelid is backed by hyaline cartilage to which the cornea lies in juxtaposition. The integument opposite this cartilage is unpigmented in a roughly circular area centrally located near the free margin of the lower lid.

The lower eyelid of *Uma* was removed and examined under the microscope. It was found that the unpigmented area in the lid transmitted light to a much greater extent than did the remainder. Comparative work was done on other Southern California lizards and it was found that certain other species appeared to have a similar, though in all cases examined a less well developed, light-transmitting region. The position of the pupil of the eye relative to the lower lid is such that it receives light waves through the translucent area when the eye is closed.

Thus, we have, in *Uma*, a tendency which has reached its peak in the snakes and certain lizards which are without moveable eyelids. An intermediate stage is found in certain desert skinks. Barbour (1926) mentions the presence in these animals of a spectacle in the lower eyelid, which permits vision when the eye is closed, and at the same time makes possible protection against blowing sand. In some cases this window is a simple round disc; in others it occupies the whole eyelid and the lid itself is permanently closed and fused with its fellow. Barbour points out that it is invariably the lower lid that is modified in this way. The degree of translucence is not great enough to permit the perception of objects in *Uma*, but the detection of a passing shadow or other marked change in light intensity may be possible.

#### Nictitating Membrane

The adaptive features of the structure and functioning of the eyelids associated with protection of the eyes from foreign matter have been discussed; however, there is yet to be considered the important part played by the nictitating membrane and associated structures in the elimination of occasional inured particles.

Although the eyelids are effective in preventing the entrance of most wind-blown sand as well as in the obstruction of grains during subsurface locomotion, nevertheless some particles gain access to the eyes. The third eyelid or nictitating membrane is concerned with the removal of these fragments, which if allowed to accumulate, would result in discomfort and ultimately serious impairment of vision.

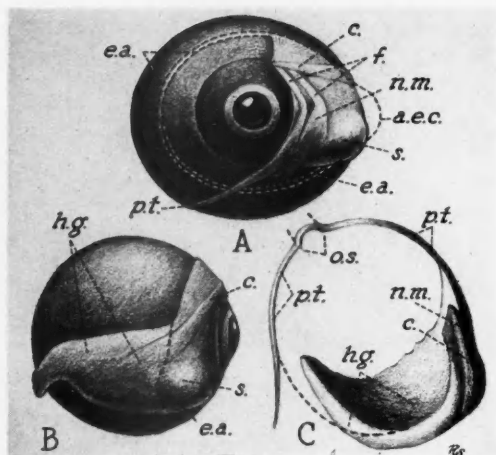


Fig. 7. A. External appearance of the nictitating membrane of *Uma*. The right eye has been removed with the membrane intact. B. Anterior surface of the left eyeball of *Uma*. C. The nictitating membrane, including its tendon, and the Harderian gland have been removed as a unit. The position of the eyeball is indicated by the broken line. (See Fig. 9 for explanation of abbreviations.)

#### Sand Elimination from the Eye

It is common experience in examining the eye region of *Uma* to find considerable sand in the anterior corners. The small diameter of the lacrymal ducts and the position of their orbital orifices, made removal of sand particles by drainage into the buccal cavity seem unlikely. Observation of captive animals finally led to the discovery of the mechanism involved.

While watching several captive individuals, attention was attracted to one animal which was violently protruding its eyes. In the midst of this behavior a whitish opaque object appeared at the anterior corner of the eye and was thrust out onto the eyeball by a glistening reddish tissue which appeared and disappeared several times. The animal then reached forward with the hind foot and scratched away the pellet which was adhering to the surface of the cornea. This was followed by a scratching motion of the other hind foot which suggested that the discharge had occurred from both eyes. Subsequent observation revealed that sand masses may be ejected simultaneously.

Examination of the toe-nails revealed that their configuration is such that when the foot is brought forward, the flattened surface of the nails are parallel to the surface of the cornea. This reduces the possibility of injury to the eye from scratching.

Bruner (1907) describes a *sinus membranae nictitantis* occurring in the Lacertilia. This sinus is a part of the system of cephalic sinuses mentioned previously in connection with intumescence of the eyelids.

The device for cephalic blood-pressure control is intimately associated with the sand-elimination mech-



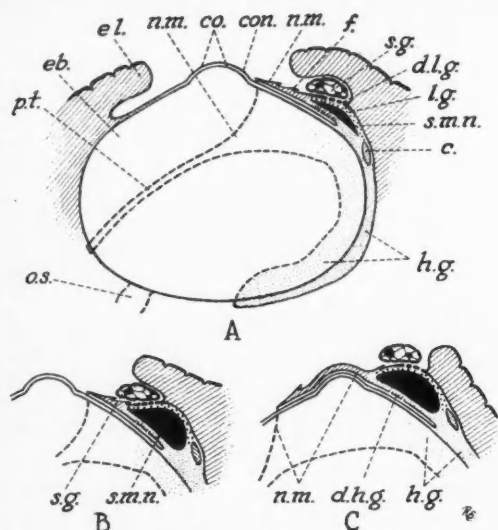


FIG. 8. Diagrams illustrating the mechanism for sand elimination from the anterior eye corner in *Uma*. A. Frontal section through the eye region of *Uma* showing the position of the nictitating membrane when relaxed. B. The blood sinus at the base of the membrane is distended with blood. C. The membrane has been projected out over the eye. The swelling at its base impinges on the sand mass, forcing it out of the eye corner. (See Fig. 9 for explanation of abbreviations.)

anism. The reddish tissue appearing at the base of the nictitating membrane during the process of elimination is the distended blood-filled sinus (Fig. 8, B, C).

Bruner states further that irritation such as that which arises from a loose piece of skin in the orbital region induces functioning of the "swell mechanism," therefore it is probable that accumulated sand particles in the eye corner may likewise function to initiate the action of this mechanism.

The agglutinated sand-grains in the anterior corner of the eye are pushed out on to the cornea by the swelling at the base of the nictitating membrane (Fig. 8, C). This occurs as the membrane is moved posteriorly over the eye surface. The portion which comes into contact with the sand particles is protected by a relatively thick stratified epithelium (Fig. 9, *t.s.e.*).

The protrusion of the eyeball aids in the removal of the pellet by increasing the pressure on the foreign material. This pressure tends to force the mass out on to the cornea. Since the deposit is encapsulated by mucous it is readily moved in this direction. The lubricating mucous film prevents scratching and abrasion of the delicate conjunctival surfaces.

Experimentally particles of sand have been dropped on to the surface of the eye. The nictitating membrane has been observed to catch these grains on its free edge and carry them out of sight into the posterior eye corner. But, the particles tend to adhere to the moist and somewhat sticky edge of the

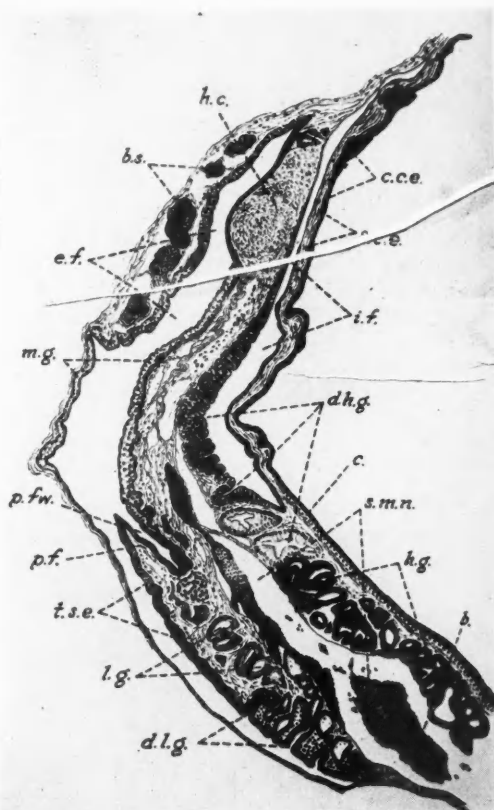


FIG. 9. Transverse section through the basal portion of the nictitating membrane showing its microscopic structure. The eye lies on the right in the diagram. *a.e.*, place of attachment of eyelids; *b.*, blood; *b.s.*, blood sinuses; *c.*, cartilage; *c.c.e.*, choroid coat of eye; *co.*, cornea; *con.*, conjunctiva; *d.h.g.*, duets of the Harderian gland; *dl.g.*, duets of the lacrymal gland; *e.*, eye; *e.c.*, eye corner; *e.f.*, external fornix; *el.*, eyelid; *f.*, dorso-ventral folds; *h.c.*, hyaline cartilage; *h.g.*, Harderian gland; *i.f.*, internal fornix; *lg.*, lacrymal gland; *m.g.*, mucous glands; *n.m.*, nictitating membrane; *o.s.*, optic stalk; *p.f.*, dorso-ventral fold; *p.f.w.*, dorso-ventral furrow; *p.t.*, pyramidalis tendon; *s.*, swelling (due to glandular elements and distended sinus of the nictitating membrane); *s.c.e.*, sclerotic coat of eye; *sg.*, sand grains; *s.m.n.*, sinus membrane nictitantis; *t.s.e.*, thickened stratified epithelium.

membrane, and they are usually drawn back across the eye with deposition occurring anteriorly rather than posteriorly. Further, the surface of the membrane adjacent to its free edge is troughed in such a manner that particles may be caught in these furrows to be carried forward (Fig. 7, *f.*, 8).

*Uma* is not unique in this method of sand elimination. A similar mechanism is inferred for *Uta stansburiana* and *Callisaurus draconoides gabbi* on the basis of sand pellets found in the eye corners. It is my opinion that this device may be quite general among lizards. It is of special importance, however, in sand-dwelling forms.

*Structure of the Nictitating Membrane*

Following the observations on the action of the nictitating membrane in the avoidance of sand pellets, attention was directed toward its structure, in an effort to obtain a clearer conception of its function and relationship to the eyelids and other orbital features.

Conspicuous features of the membrane as represented by *Uma* are: (1) The highly vascular nature of portions of the tissue; (2) the troughs which open anteriorly and extend in a dorso-ventral direction across the membrane; and (3) a prominent supporting bar of hyaline cartilage that conforms to the curvature of the eyeball and is imbedded in the upper portion of the membrane.

*Gross Morphology*

The shape of the membrane in *Uma*, as in other reptiles and in birds, is roughly triangular. The one free corner is prolonged diagonally ventro-posteriorly as the pyramidalis tendon (Fig. 7, A., *p.t.*). This tendon is broad and flat, lying close to the eye, and is discovered with difficulty in gross dissection. It passes dorsally to the optic stalk and in contact with it. The tendon passes around the globe, attaching in an antero-dorsal position on the interorbital septum.

In *Uma* the palpebral surface possesses two rather prominent dorso-ventral folds (Fig. 7, *f*). One lies adjacent to the first and somewhat more anterior in position. These folds are free along their anteriorly directed edges, but not posteriorly. In a frontal section of the eye region then, the surface of the nictitating membrane would appear to be barbed (Fig. 8). The ventral portion of the second fold is located on the side of a prominent swelling which appears at the base of the membrane where it attaches loosely to the anterior eye corner (Fig. 7, *s*). A prominent supporting cartilage bar extends horizontally across the upper part of the membrane.

During periods of intumescence, the swelling just described becomes more pronounced, and numerous blood channels appear beneath its surface. Similar blood channels become conspicuous along the dorso-ventral folds previously mentioned.

The base of the nictitating membrane in *Uma* is invaded by two glands. The Harderian gland is largely ventral in position and embraces the anterior portion of the globe (Fig. 7). It extends some distance posteriorly behind the eyeball and invades the base of the nictitating membrane adjacent to its internal surface. Ducts empty its secretion into the internal fornix (Fig. 9). The lacrimal gland is located at the base of the membrane beneath its palpebral surface, opposite the Harderian elements. Its secretion is poured into the external fornix. Between these glands and among their tubules is found the greater part of the *sinus membranæ nictitantis*.

It is primarily these glands which give prominence to the base of the nictitating membrane when undistended with blood. The blood channels which appear in this tissue and in the folds of the palpebral sur-

face are the result of engorgement of the sinus membranes nictitantis and its ramifications.

A detailed description of the micro-anatomy of the membrane would serve little purpose. Attention to the illustration (Fig. 9) will give the essential information on this aspect of structure. It may be pointed out, however, that the basal portion of the membrane which habitually comes into contact with sand-grains is covered with a somewhat thicker stratified epithelium.

## THE PARIETAL EYE

Although the parietal eye of existing *Laecertilia* is generally considered as a "degenerate" or vestigial organ, the external appearance of the structure in *Uma* is so strikingly like that of the paired eyes that functional possibilities were suspected (Fig. 10). Certain aspects of the behavior of *Uma* further encouraged this suspicion.

The lizards frequently lie buried beneath the sand with only the top of the head exposed. When so submerged the parietal eye is in a position to receive light at a time when the paired eyes are covered with sand. These facts seemed to be of sufficient importance to warrant a rather extensive study of the organ.

*Morphology of the Parietal Organ in the Genus  
Uma—External Morphology*

The parietal eye of *Uma* is located dorso-medially on the head, just posterior to the eyes. The pineal scale, in which the eye is situated, may be as much as 2 mm. in diameter in an adult animal and is surrounded by many small, almost granular, scales which form a bed in which the parietal plate stands out in contrast (Fig. 10).

In dorsal aspect, the scale is usually slightly concave, with a median conical elevation which may be designated as the corneal papilla, since it resembles the cornea of the functional vertebrate eye. Chromatophores are absent in this region but are present peripherally in the scale tissue. The integument which comprises the cornea is transparent, making it possible for one to see certain of the internal features of the eye through this tissue.

Upon examining the parietal eye of *Uma* under the dissecting microscope, the striking resemblance of the organ to a functional eye is apparent. A black spot is present which resembles a pupil about which is found a circular yellowish region suggestive of an iris. However, this similarity in structure is for the most part only apparent as will be made clear later.

*Relationship of the Parietal Eye to Adjacent  
Structures (Skull and Brain) (Fig. 11)*

The pineal foramen of the skull of the adult may vary in shape but is often triangular with one angle directed posteriorly (Fig. 12). Its anterior side is formed by the frontal bone; the other two by the parietals. Its greatest measurement (usually along

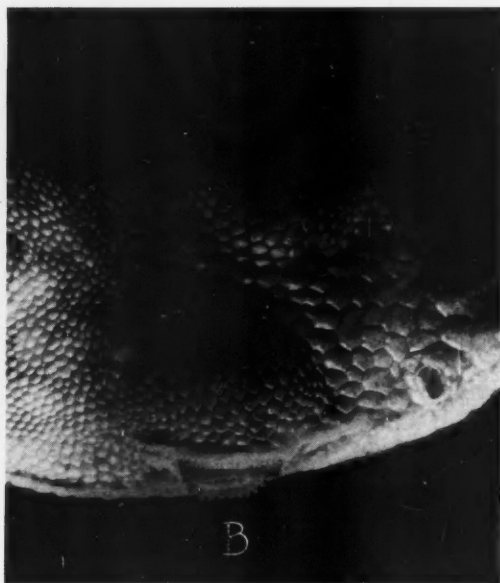
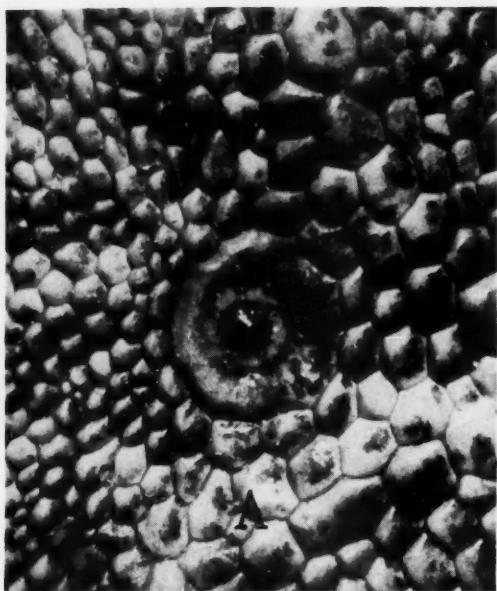


FIG. 10. A. Close up of the parietal scale of *Uma inornata*. The parietal vesicle lies beneath the central transparent area, appearing as a black pupil-like spot surrounded by a lighter iris-like area. B. Dorsal aspect of the head of *Uma inornata* showing the position of the parietal scale. (Photos by R. B. Cowles.)

the anterior margin) corresponds roughly to that of the pineal scale which lies directly above it. The parietal bones posterior to the eye are relatively thin, and even in adult animals frequently may be unossified centrally, so that there appear additional openings in the bone of the cranial roof. In young individuals the cranial roof is ossified at the periphery only, the greater part of the dorsal surface of the cerebral region of the brain being without a bony covering (Fig. 12, B).

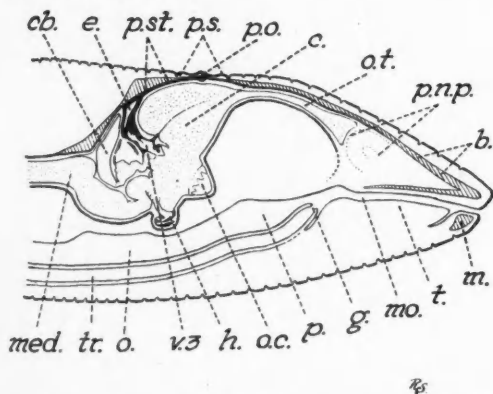


FIG. 11. Median sagittal section through the head of *Uma inornata* showing the relationship of the parietal eye to the brain. b., bone; c., cerebrum; cb., cerebellum; e., epiphysis; g., glottis; h., hypophysis; m., mandible; med., medulla; mo., mouth; o., oesophagus; oc., optic chiasma; o.t., olfactory track; p., pharynx; p.n.p., position of the nasal passage; p.o., parietal organ; p.s., parietal scale; p.st., parietal stalk; v. 3., 3rd ventricle.

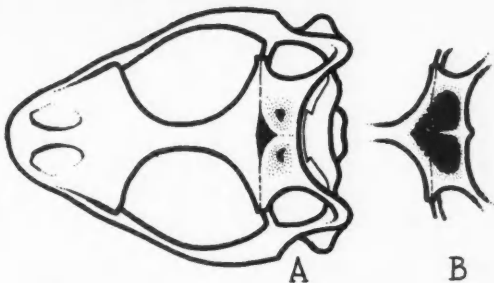


FIG. 12. A. Dorsal aspect of the skull of an adult *Uma inornata*, showing the size, shape, and position of the pineal foramen. Note the incompletely ossified parietal bones (stippled areas). B. Cranial region of a juvenile. Note the extent of the unossified area.

In addition to the periosteum, the bones of the cranial roof are covered externally by the integument and internally by the heavily pigmented dura mater of the brain. These layers come into contact in the region of the pineal foramen. The parietal vesicle (to be described in detail later) appears to lie in contact with the subepidermal tissue of the integument in the mid-region of the pineal scale. Pigmentation of the dura mater ends rather abruptly a short distance within the boundaries of the overlying parietal plate. Since few chromatophores occur in the skin near the corneal papilla, an area of translucence appears about the parietal vesicle. This is readily appreciated when the brain roof with its bone and membranous layers intact is held up to a source of light. If viewed in this manner, a halo of trans-

lucence is seen about the parietal vesicle. The vesicle appears as a black dot set off from the opaque heavily pigmented brain roof by this ring of transmitted light. Thus light may penetrate to the cranial cavity, illuminating the brain at the pineal foramen.

Since the parietal eye is situated above the anterior portion of the cerebral hemispheres, it is this portion which is most directly illuminated (Fig. 11). Possible implications associated with this phenomenon are discussed on a later page.

*Microscopic Structure (Fig. 13)*  
*Parietal Vesicle*

The morphology of the adult parietal eye of *Uma* is comparable in its general relationship to that of the functional lateral eyes of vertebrates. There is present a corneal region, a well defined lens, an inner chamber between the lens and the retina, possessing a vitreous body, and a distinct retinal layer which is backed by an investment of connective tissue. These are structures associated with well developed visual receptors.

Conspicuous discrepancies in general form as compared to the functional eye are, however, readily noticed. There is no structure which can be compared with an iris; the anterior and posterior chambers of

the eye are completely absent, the convex externally directed surface of the lens being in direct contact with the corneal tissue; and pigmentation is heaviest toward the inner portion of the retina in the position occupied by the fiber zone of the functional eye. These pigment granules stand between the source of light and the retinal cells, rather than behind the sensory layer, as in the functional vertebrate eye. No technical treatment has been employed capable of revealing any nervous tissue in the pineal stalk which connects the eye with the brain and the existence of such tissue is therefore exceedingly doubtful.

*Cornea*

The corneal region is composed of an integument similar to that which covers the body as a whole. It appears as a low conical elevation approximately central in location in the pineal scale. The tissue of the scale and cornea is continuous and is similar in structure. However, the epidermis of the integument tends to be somewhat thicker in the region of the corneal elevation, thinning peripherally. The stratum germinativum of the corneal tissue is composed of several cell layers. The innermost possesses for the most part rounded nuclei. The nuclei in the layers above this basal stratum tend to be elliptical in shape, many of the outermost becoming elongate,

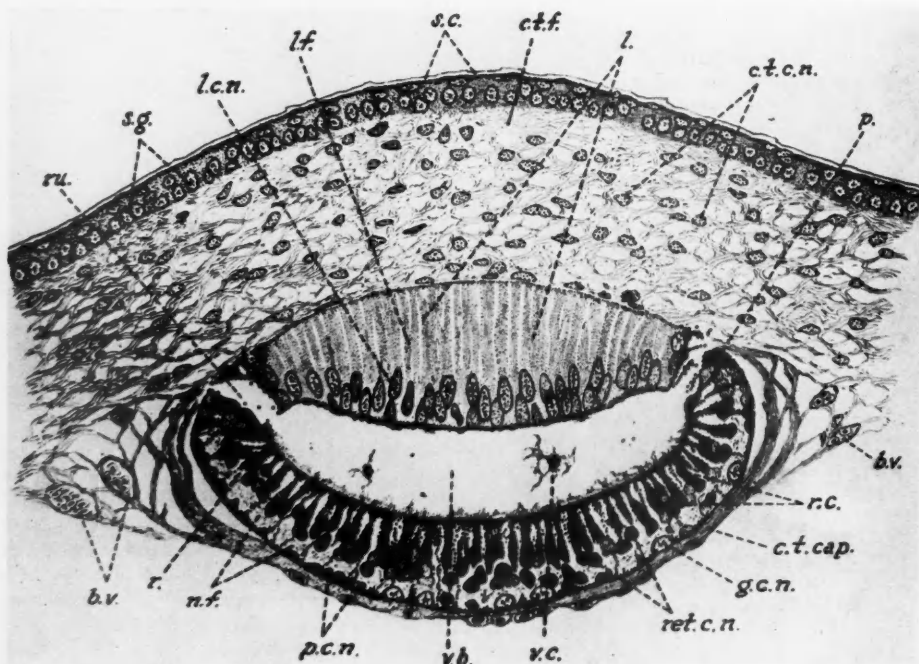


FIG. 13. Transverse section through the parietal eye of *Uma inornata*. b.v., blood vessel; c.t.c.n., nuclei of connective tissue cells; c.t.cap., connective tissue capsule; c.t.f., connective tissue fibers; g.c.n., nucleus of ganglion cell (Ritter's zone II); l., lens; l.c.n., nucleus of lens cell; l.f., lens fiber; n.f., nerve fibers (Ritter's zone III); p., pigment; p.c.n., nuclei of pigment cells; r., retina; r.c., rod cells (Ritter's zone V); ret.c.n., nuclei of retinal cells (Ritter's zone IV); ru., rupture in wall of parietal vesicle; s.c., stratum corneum; s.g., stratum germinativum; v.b., vitreous body; v.c., vitreous cell.



a few adjacent to the stratum corneum appearing as amorphous elongate darkly staining objects. The thin stratum corneum is translucent, with few nuclear remnants (Fig. 13).

The sub-epidermal tissue of the corneal region possesses no chromatophores although these structures are abundant in adjacent areas. Ritter (1890) observed a similar absence of pigment in this region, in his investigation of *Phrynosoma douglassii*, *P. coronata*, and *Uta stansburiana*.

#### Lens

The lens is a well-formed structure. It is biconvex in shape, the outer curvature often slightly more pronounced than that of the interior face. In microscopic sections it may be distinctly separated, laterally, from the retinal wall, but this is due to rupturing of the tissue at the point of contact between the lens and retina. In the living state the lens is continuous with retina, and the space observed in preserved material is due to shrinkage. Its inner face is free, projecting into the cavity of the vesicle. The outer surface is in direct contact with the sub-epidermal tissue of the cornea.

The cells which compose the organ are much elongated, suggesting the fibers of functional lenses (Fig. 13, *l.f.*). The nuclei of these cells are relatively large and are predominantly elliptical in shape. They are most numerous near the inner surface, becoming progressively less abundant toward the external face. Nuclei are usually completely lacking adjacent to the external surface. The disposition of nuclei and the appearance of the lens fibers suggest a columnar epithelium, with the nuclei tending to occur in a basal position in the cells. The distal ends of the lens fibers are directed toward the corneal tissue.

In some lizards pigment has been found in the lens. None of the *Uma* examined exhibited this condition.

#### Cavity of the Vesicle

The shape of the vesicular chamber of the parietal eye resembles in section the letter C. A cast of this cavity would appear as a shallow cup. The material of the cast would be thickest through the center of the bottom, thinning peripherally. The distance from the inner surface of the lens to the surface of the retina is usually about the same as the width of the lens.

The parietal cavity possesses a vitreous body which has been revealed both by gross dissection and microscopic study. The presence of a substance comparable in position and general composition (i.e., presence of cells (Fig. 13, *v.c.*) and viscosity) to the vitreous humor of the functional eye has thus been established.

#### Retina

The retina is a shallow cup-shaped structure, thickest centrally. In life, it is continuous with the lens. I find it comparable to the structure in *Phrynosoma douglassii* described by Ritter (1890) and to the

parietal organ of *Anguis fragilis* described by Nowikoff (1910). Following the plan of description used by Ritter, certain retinal zones are encountered as one proceeds internally from the external surface of the vesicle. The external limiting membrane (or basement membrane) described by Ritter for *P. douglassii* was not convincingly demonstrated for *Uma* but it is probably present. The second zone, which is characterized by a single layer of rather large round nuclei sparsely placed and heavy pigmentation in *P. douglassii*, is present in *Uma*, but pigmentation is slight. This zone is the region in which ganglion cells were found by Nowikoff. The cells present in *Uma* in this area appear to be of this type. This zone is followed by a narrow region (Ritter's zone III) which is essentially free from nuclei but with pigment granules present in small numbers. Ritter described this zone as unpigmented in *P. douglassii*. It corresponds to the nerve fiber region of Nowikoff. Nerve fibers are present in this region in *Uma* (Fig. 13, *n.f.*). Ritter's zones IV and V, based largely on differences in nuclear shape, are likewise present. In *P. douglassii* zone IV is characterized by many round nuclei and zone V possesses elongate nuclei, many of which extend to the internal limiting membrane of the retina. Both of these zones also occur in *Uma* (Fig. 13, *ret. c. n.* and *r. c.*). The latter zone is composed of rod cells according to Spencer (1887) with numerous pigment granules usually obscuring the region. Heavy pigmentation in this area is also described for *Anguis fragilis* by Nowikoff. In *Uma*, pigment is likewise abundant at this level of the retina. These granules, which appear to be identical in nature with those found in the chromatophores of the skin, in the dura mater, and in the epiphysis of the brain reach a tremendous degree of concentration in this region. It is difficult to see how light stimuli could be transmitted to retinal receptors through this interposing screen unless there were a shift in the position of the pigment at the time of stimulation.

Several small blood vessels pass from the epiphysis to the parietal eye. However, there appears to be little vascularization of the tissue about the vesicle which stands in contrast to the condition found by Ritter in the two species of *Phrynosoma*.

The parietal vesicle is surrounded by an investment of connective tissue which, laterally, appears to be continuous with the connective tissue of the dermis. This investment is extremely thin between the lens and the cornea and rarely can be differentiated from the tissue of the corium.

#### Pineal Stalk (Fig. 11)

In adult as well as juvenal lizards a definite connection exists between the epiphysis and the parietal vesicle. Although the pineal stalk is extremely slender, it is large enough to be easily seen with the unaided eye, in diameter appearing about as big as a human hair. In the fresh condition it is yellowish-white in color. Frequently I have dissected out the



stalk from its attachment to the roof of the cranial cavity, using only macrodissection technique.

The stalk originates from the anterior end of the epiphysial vesicle (Fig. 11, e.) and becomes somewhat more slender in the region of the eye. It is held in place by connective tissue fibers which bind it to the cranial roof throughout its length. Pigment granules tend to accompany it across the translucent area to the parietal vesicle.

As a rule with adult lacertilians the parietal nerve, which passes from the retina of the eye to the commissura habenularis of the brain, has been lost. But Spencer (1886 and 1887) and others hold that there is a nervous connection between the brain and vesicle in *Lacerta*, *Sphenodon*, and *Varanus*. Leydig (1889), referred to by Spencer, disagrees, however, with this conclusion for *Varanus* and *Lacerta*, and claims that in these cases the structure is not a nerve but rather a strand of connective tissue. Strahl and Martin (1888) and likewise Francotte (1897) likewise mentioned by Spencer, describe a nerve for *Anguis fragilis*.

Nerve fibers have not been convincingly demonstrated in *Uma*. The pineal stalk in this genus appears to be essentially a connective tissue strand, accompanied by several small blood vessels which appear to enter the connective tissue investment of the retina. Nevertheless, on the assumption that a nervous connection does exist between the brain and the pineal eye several functional possibilities for this organ may be considered.

The structural similarity of the organ as compared with the functional paired eyes, suggests that the pineal eye may act as a photoreceptor. Clausen and Mofshin (1939) claim such a function in the lizard *Anolis carolinensis*, on the basis of oxygen-consumption studies. According to these observers the pineal proved to be of less importance in photo-reception than retinal and dermal receptors, but analysis of statistical data indicated that the organ functions as an agency for the perception of light in this species of lizard.

Further, the organ may have secondarily become a thermo-receptor. The lens may serve to concentrate rays of infra red light on the highly pigmented retina. The dark pigment granules which are clustered about the receptor cells would tend to absorb heat or invisible light. The stimulation transmitted to the adjacent receptor, then, would be a thermal one. Attempts to demonstrate by means of photographic plates the absorption of infra red vibrations by the parietal organ have yielded only negative results.

The life activities of reptiles are dependent on temperature. No specific organ has been associated with thermo-reception in the Lacertilia, the skin being generally accepted as reacting to thermal sense stimuli. Animals so dependent on temperature might possess a specific organ for the detection of thermal changes. Thus as early as 1886 Rabl-Rückard suggested that the parietal organ might be of use in furnishing its possessors with more delicate means of

detecting differences of temperature than exist anywhere else in the body.

A still further possible function has been associated with this organ by Ritter (1890). According to this writer, blood sinuses in the pineal region of certain lizard species suggest a physiological function for the organ. In *Phrynosoma douglassii* such blood spaces appear to occur in the retina. In *P. coronata* they occur there and also beneath the organ. In many lizards a blood sinus is situated above the epiphysis. Only the epiphysial blood sinus appears to be well developed in *Uma*.

#### Experimental

With the previously mentioned functional possibilities in mind, an experiment was devised to test the validity of certain of these speculations.

Although, as a consequence of the anatomical studies, the nervous nature of the pineal stalk was much in doubt, the following experiment was performed in an attempt to obtain a response through stimulation of the retinal cells of the parietal organ.

Sunlight was admitted to a darkened room through a small aperture in a southeast facing window (Fig. 14). This light was directed from outside by a sys-

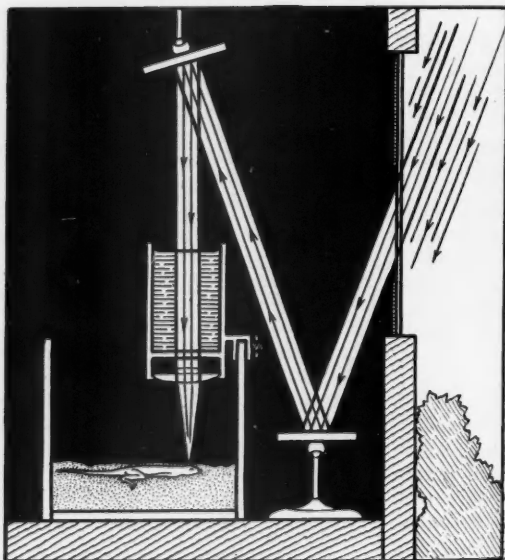


FIG. 14. Apparatus used in projecting a pin point of sunlight on to the parietal organ of *Uma*.

tem of mirrors into a sand box occupied by *Uma*. The light from the last mirror was reflected down through a water chamber, which was used to absorb heat, and then through a large, 4-inch, simple magnifying glass which was employed to project a pin point of light onto the surface of the sand. With a camel hair brush the operator carefully dusted the sand from the head of a buried lizard exposing only the parietal organ. The amount of water in the heat-

absorbing chamber was adjusted until the temperature of the point of light was comfortable to the fingertip. The light was then brought to bear on the parietal eye. The lizard evidenced no outward sign of any stimulation. This experiment was repeated many times on different individuals at different body temperatures, all with negative results.

The temperature of the light was increased to a point which caused the animals, after a few moments irradiation, to jerk the head under the sand. The region of the parietal organ did not appear to be significantly more sensitive to heat than other parts of the integument in the cranial region.

### Conclusion

The study of the parietal organ in *Uma* lends support to the general view that in all living forms the third eye is an organ which has undergone retrogression. Although the vesicle is well developed in *Uma*, the pineal stalk is little more than a slender connective tissue strand. If nerve fibers are present, they are exceedingly few in number.

On the other hand, reflection on the habits of the lizards suggests a probable function performed by the general area occupied by the organ. The translucence of the integument surrounding the vesicle and the thinness of the cranial roof, bone being largely absent in this region in juvenals and very thin in adults, bring the dorsal surface of the brain into proximity to external changes in temperature. Suitable temperatures are necessary for the maximum functional efficiency of the brain as well as of the effectors, muscles and glands. It is important that the brain and the nervous system be ready to operate when the muscles and other tissues have warmed up to the point of efficiency. A lag between these events would lead to uncoordinated and ineffective movements. The clumsy uncertain movements of a lizard which has been disturbed on a cold morning are familiar to most students of reptiles. This lack of coordination is probably due as much to the condition of the nervous system as it is to that of the effectors.

In nature a submerged lizard, which has passed through the low temperature of a cold night, is warmed into activity by the penetration of warmth from the sun's rays. The brain, covered by little more than a thin layer of integument, would readily become warm and would be ready to function in coordinating the movement of the muscles.

### HEARING

Detailed studies have not as yet been carried out on the anatomy of the middle and internal ear of *Uma*. Observational and experimental data suggest, however, an acute auditory sense in these animals.

The following observations were made on captive specimens.

#### Subsurface Detection of Sound

During the feeding of a single individual, several other buried lizards responded to vibrations pro-

duced in the sand by the surface movements of meal worms (*Tenebrio molitor* larvae). One worm, which had escaped the notice of the feeding lizard, began to crawl across the sand to one side of the cage. The head of a subadult *Uma* broke through the surface adjacent to the route of this larva (about 8 cm. distant). The animal looked about alertly for a moment and then dashed out of the sand to seize the prey. A second buried lizard responded in a similar fashion as a meal worm approached its position.

On another occasion the behavior of a submerged lizard in response to sounds suggested the possibility that the animals may be able to determine, with accuracy, the location of insect food on the surface. A well-developed directional sense appears to be present.

The location and orientation in the sand of an adult individual was known. A meal worm was placed on the surface directly back of the lizard, about 3 inches behind the animal's head. The worm was kept in this location by probing with a slender wire. After a few minutes the lizard broke suddenly from the sand and, almost in one movement, wheeled about and seized the food.

Further support for the probability of directional sound-determination through sand came about accidentally. A meal worm had been dropped into a shallow depression near which a lizard was known to have buried itself. Before the expected response of this animal, a juvenal appeared in a depression some 15 inches away. This individual ran over the hump between the two depressions to seize the meal worm. There was no hesitation or observable uncertainty as to the location of the food; the lizard ran directly to the prey, the location of which must have been determined by some other means than sight, since a heap of sand obstructed its vision.

Buried lizards responded to a medium-pitched whistle. On numerous occasions it was possible to cause submerged animals to lift their heads out of the sand in response to whistled notes. It is possible, however, that the vibrations may have been amplified by vibration of the sides of the box in which the lizards were housed. This box was 30 x 30 x 120 cm. made of 1/2-inch white pine lumber. The entire front was heavy glass. The top was hinged and kept open during experiments. About 4 inches of sand was placed in the bottom of the cage.

A number of times a shrill whistle (not a pure tone), about 515 vibrations per second, stimulated animals to submerge. Such individuals showed, by movements, obvious discomfort or uneasiness from the sound, before resorting to submergence. On the other hand, on several occasions buried animals emerged from the sand following such whistles or were stimulated into shifting their positions without coming to the surface.

#### Surface Detection of Sound

Satisfactory evidence has been gained that *Uma* can detect sounds transmitted through the air. On many occasions the closed eyes of lizards basking

under a lamp placed at one end of the cage were opened in response to a whistle or snapping of the fingers.

The ability to detect, while submerged, the sounds produced by animals on the surface is of value for *Uma* in the procurement of food and in avoiding enemies.

Since *Uma* can produce a sound when sand is expelled from the nasal passages, following a period of submergence, the possibility of communication between these animals suggests itself but no data have as yet been obtained to support this view.

#### LOCOMOTION

Locomotion of *Uma* within its aeolian habitat may be considered from two aspects, subsurface or fossorial locomotion and surface movements. The modifications in body form, scalation, and limbs are such as to facilitate progress on and within the loose substratum.

#### Surface Locomotion

*Uma* moves over the surface of the sand with the limbs operating in the primitive position, i.e., extending out to the sides rather than under the body. Although the lizard is relatively heavy-bodied and the soil loose, it is capable of attaining a surprising speed over the sandy surface. One medium sized individual was clocked at twelve miles per hour on one occasion.

When an individual is running rapidly most of the weight is supported by the hind limbs, the front feet being used only occasionally to aid in maintaining balance. The tail is elevated off the sand but the tip may occasionally touch the ground. Movement is thus essentially bipedal during accelerated locomotion.

When the animal moves more leisurely, all four feet are placed on the ground, but the appearance of the footprints suggest that most of the body weight is borne by the hind feet.

Mosauer (1935) and others have pointed out that the digital fringe scales give an increased surface to the foot and thus greater support on a shifting substratum (Figs. 18, 19). Examination of the tracks made by *Uma* and observation of animals which were moving slowly enough over the sand to permit scrutiny of foot action lead to doubts concerning the validity of this interpretation. It was thought from these observations that the animals ran on their heels rather than on their toes. An experiment was devised to make clear the action of the foot in rapid locomotion over the sand.

Sandy soil provides inadequate impression for study, the imprint of the individual toes not showing. Therefore, a mud plot (3 x 4 meters) was prepared of such consistency that a slight contact, even of a small object, would leave a mark in the mud. An adult *Uma* was then tethered on the end of a 6 meter length of string. The animal was sufficiently warmed so that it exhibited what appeared to be normal activity. This individual was placed at one

end of the plot and released. It ran quickly across the mud until restrained by the string—held by the experimenter. The tracks made were thereupon examined. The marks produced proved earlier observations to be correct. The imprint of the toe nails and the toes was conspicuous. At no place could a well defined heel mark be discerned though the experiment was repeated several times, using different individuals. The weight of the animal was being supported almost entirely on the toes. Fig. 15, B

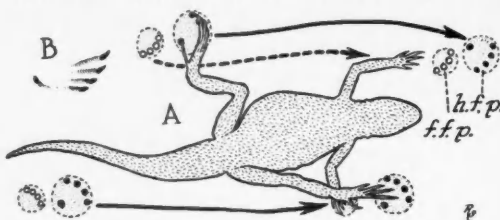


FIG. 15. A. Diagram depicting the movements of the limbs during surface locomotion in the genus *Uma*. Compare the track produced with that in Fig. 16. B. Foot print of *Uma* copied from the impression of the hind foot in mud.

shows the imprint of the hind foot as made in the mud. Note that at no point does a heel mark appear. The fringe-scales are operative in surface locomotion. Thus the observations of Mosauer and others were confirmed.

Tracings in the mud produced by the tail appeared consistently only in the first part of the track. Apparently as the lizard got up speed the tail was elevated, so that it rarely touched the ground.

The tracks left by an animal are often of considerable value to the field naturalist in piecing together information on its activities. Information on size of the individual, speed and direction of movement, behavior, encounters with enemies, etc., can be obtained by "track reading." An interpretation of the marks produced by *Uma* in surface locomotion follows:

Although the lizards run on their toes, the loose substratum of the habitat retains little impression of the individual digits (Fig. 16). Instead, a rounded depression is produced which can be easily duplicated by poking a finger into the sand. It was the shape of this mark that had suggested the heel-running type of locomotion.

The impressions made by the hind feet are several times larger than those of the forefeet. As was mentioned earlier, the forefeet are used infrequently in rapid locomotion. When employed, marks produced by them usually appear behind those of the hind feet or, in some cases, they may be partly obliterated by the superposition of the impressions of the latter. On the right-hand side of Figure 16, a mark made by the right forefoot can be seen posterior to that made by the posterior limb.

#### Sand-swimming Activities

The directional movements of a fossorial animal may be considered from two aspects, viz.—(1) dis-



FIG. 16. Track made by *Uma* when running over the sand. The direction taken by the lizard can be determined by noting the position of the occasional marks of the front feet. They occur posterior to the impression of the hind foot. The small dent in the sand on the right of the picture was made by the right fore-foot. The undulating mark between the foot prints was produced by the tail. Relative size is indicated by the 5 cent piece. (Photo by R. B. Cowles.)

placement in a horizontal plane, and (2) shifts in position vertically. In *Uma*, subsurface locomotion appears to be confined to very limited movements in both of these planes. Mosauer (1935) states that he has never seen *Uma* move horizontally in the sand for distances greater than several times the total length of the lizard. I have found no movements to exceed this. The animals do not swim, mole-like, beneath the surface, except to a very limited extent. Ordinarily forward progress ceases when submergence is complete.

Movement vertically is frequently limited by compacting of the sand below a loose superficial layer, 5 or 6 cm. thick. Capillary water, seeping up from below, cements the sand particles weakly below the surface. In sand-swimming the lizards confine themselves largely to this dry loose surface material. This method of locomotion is such that, by this means, only the penetration of loose material appears to be possible. Captive animals are unable to submerge in sand which has been thoroughly wetted. Sand-swimming is restricted when the sand is moistened by rains. At such times the lizards may excavate their own burrows or retreat to those made by certain rodents such as *Citellus* or *Dipodomys*.

When the animals are warm they move so quickly in swimming into the sand, that they appear to plunge beneath the surface in one movement. Colder, more slowly moving individuals give a better picture of the sand-swimming response. The pattern of behavior is constant in sand submergence, and is a similar one regardless of its speed of execution. In rapid submergence the several movements involved are performed so quickly that they may be missed.

In diving into the sand, *Uma* employs a downward thrust of the shovel-shaped head accompanied by rapid and vigorous lateral movements executed by the

well-developed muscles of the neck region. The shape of the sides of the head are important in submerging by lateral movements (Fig. 4). The sides of this organ possess a ridge which facilitates its movement through the sand. The rostral and upper labials are associated with this projecting sharp edge. The edge divides the surface of each labial shield into an upper part, facing up and sideways and a lower part, facing downward. The lower labials are at about the same level as the lower surface of the uppers, due to the counter-sunk nature of the lower jaw. The sloping forehead serves to guide the lizard downward into the sand.

In coordination with the head and neck movements, the powerful hind limbs are alternately pushed against the soil. These limbs provide most of the propulsive force in submergence and sand-swimming since the forelegs are not employed and are appressed to the sides of the body, with the palms turned inward (Fig. 17). When submergence is accomplished,

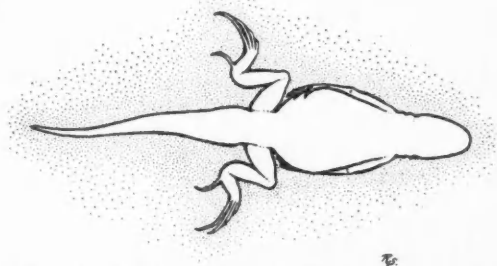


FIG. 17. Position assumed by *Uma* when at rest beneath the sand. The forelimbs are appressed to the sides, the hind limbs flexed.

the hind legs are flexed. The animal is thereby prepared for rapid abandonment of its hiding place.

As forward movement ceases, the lizards invariably vibrate the tail. The tip of this appendage is the last portion of the animal's body to become quiescent. The tail movement and the depressed nature of this organ facilitate its disappearance in the sand. The tail is usually completely concealed by this action.

The pattern of sand-swimming—lateral movements of head, forelimbs appressed to sides, propulsive action and final flexion of the hind limbs in conjunction with lateral vibration of the tail—is a behavior pattern that is well defined, recurring with little variation in both juvenal and adult lizards.

#### *Action of Foot and Fringes*

The structure and action of the hind feet and their digital fringes play an important rôle in effective sand-swimming as developed by *Uma*. The second, third, and fourth digits of the front feet are fringed with scales which increase in length progressively on the successive toes, the fourth being most conspicuously fringed. The toes of the hind feet are elongate with the second, third, and fourth progressive in development of fringes; the greatest development





FIG. 18. Right forefoot of *Uma* showing the digital fringe-scales. Note the valvular arrangement of the marginal fringe. (Photo by R. B. Cowles.)

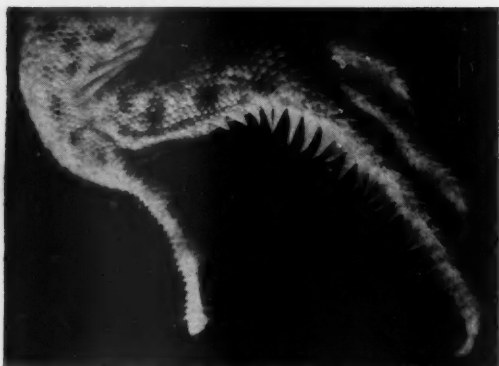


FIG. 19. Right hind foot showing the digital fringes. The foot and fringe-scales are in the position they assume when the foot is drawn forward through the sand. (Photo by R. B. Cowles.)

occurs on the posteriorly projecting scales of the fourth and longest toe; the fifth toe is without fringes (Figs. 18, 19). Cowles (1941) drew attention to the possible importance of these fringes in subsurface locomotion and pointed to the valvular nature of their action.

The following account describes the action of the foot and the valvular fringe in the propulsive movement of the hind limb:

As the foot is moved forward through the sand, it assumes the form of an entering wedge, with the metatarsal region forming one side, and the toes, extending back from their juncture with the metatarsus forming the other. The toenails are so constructed that their edges are presented to the sand as the foot is drawn forward, thus reducing the friction from these structures. The scales forming the fringes of the toes are folded back by the re-

sistence of the sand. These mechanical adjustments reduce the friction between the foot and the soil.

When the thrust of the foot is reversed for the push that propels the lizard forward, a maximum of foot surface is presented: The toes tend to form an obtuse rather than an acute angle with the longitudinal axis of the metatarsal region; the broad flat surfaces of the toenails are presented to the sand; and the fringing scales are forced out to the sides of each toe.

In connection with the digital fringe-scales, a mechanical feature tends to increase the rigidity and thus the effectiveness of these fringes when they are extended by the propulsive stroke of the foot. The scales situated on the toes dorsal to the fringe scales are relatively fixed in position and tend to brace these structures by resisting their upward movement (Fig. 20).

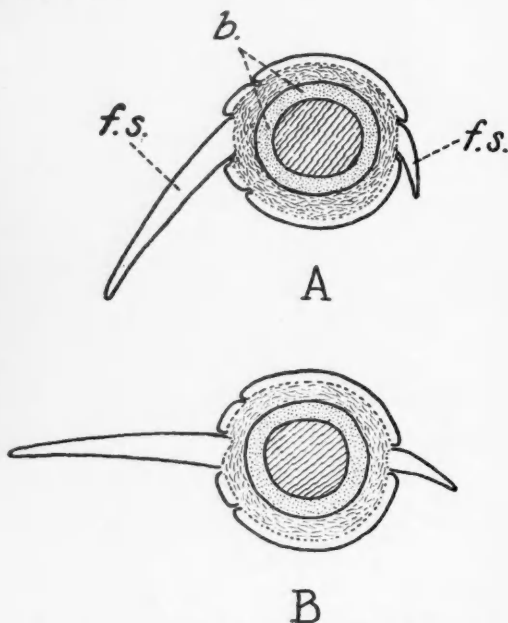


FIG. 20. Cross-section through the 4th hind toe, including fringe-scales. A. Position of digital fringe-scales when toe is drawn forward through the sand. B. Position of the scales during the propulsive stroke of the foot. *b.*, bone; *f.s.*, fringe-scale.

Over most of the body the scalation of *Uma* is smooth-granular, which reduces the friction in locomotion through the sand. But in certain limited areas, the scales are larger, acuminate, and projecting. Such regions present a rough surface to the sand during submergence. It happens that those surfaces which are moved against the soil in propulsion are those which possess these projecting scales. They occur on the shoulders, outer part of the hind leg just below the knee, and on the inner portion of the hind leg above the heel. These roughened surfaces facilitate submergence.



A paralyzed captive lizard was able to bury itself in the sand, though its hind limbs dragged helplessly. This capacity appeared to be due in part to the effective use of the roughened shoulder surfaces which were swung laterally from side to side, along with the action of the head, in the normal sand-swimming behavior of the anterior portion of the body.

The rapidity with which *Uma* is capable of submergence must be of considerable value in escaping from predators. The sudden disappearance of the animals, leaving few surface clues as to the point of burial, probably results frequently in abandonment of the prey by the predator. In collecting I have often had to remove systematically the sand in a region where a lizard had disappeared in order to collect it, because of the lack of indications as to the precise place of submergence. Unless the buried lizard is quickly uncovered, tracks and irregularities on the surface may soon be obliterated by wind action.

#### CAMOUFLAGE

As with certain other reptiles, *Uma* exhibits a striking conformity of general body-color and background. Members of the *Uma notata notata* population occupying the reddish sands of Yuma, Sandy Beach, and other regions, tend toward a reddish brown color. On the other hand, *Uma inornata* and *U. scoparia*, inhabiting whitish sands, are light-colored and difficult to see against their natural backgrounds.

In addition to this general color resemblance between the general color of the body and the sandy background, the pattern of spots further contributes to effective concealment (Fig. 1). Although these ocelli are conspicuous when the lizards are held in the hand, they merge with the scattered fragments of hornblende, mica, and other dark particles which form an important part of the sandy deposits, when the lizards are seen against such a background. At such times the animals may frequently be overlooked, until a movement indicates their presence.

The behavior of *Uma* contributes further to concealment in its habitat. As is the case with many animals when startled, the response may be such as to conceal the conspicuous shadow cast. On a number of occasions I have come upon individuals which, rather than relying on flight for escape, have depended upon their concealing coloration. The effectiveness of such coloration, however, is reduced if the shadow cast by the animal's body is not obliterated. *Uma*, as well as many other animals of depressed body form, frequently accomplish this by squatting close to the substratum, thereby essentially covering the shadow with the body.

In connection with the sand-swimming habit, the lizards may lie frequently with the body submerged but with the head elevated sufficiently to permit vision. In assuming this position, the head is lifted directly upward so that sand tends to remain on top of the organ, resulting in concealment from above.

#### FEEDING

*Uma* is primarily an insectivorous lizard, but considerable plant food is taken also. During most of the active period, food of both types is abundant in the habitat.

A summary of foods, compiled from observations on feeding lizards and from the stomach and fecal pellets, follows:

##### Animal food:

Insects  
Coleoptera  
  Tenebrionids  
  Cuculionids  
  Coccinellids  
Hymenoptera  
  Ants  
  Bees  
Hemiptera  
Orthoptera  
  Grasshoppers  
Lepidoptera  
  Caterpillars

##### Plant food:

*Larrea* (leaves)?  
*Decoria* (seeds)?  
*Cryptantha* (leaves)  
*Chilopsis* (young leaves  
and buds)

In 24 out of 30 fecal pellets investigated, were found one or more tenebrionid beetles. These insects appear to be a prominent feature of the diet of the lizards at Garnet.

##### Feeding in Captivity

Captive animals have been fed the following:

##### Animal food:

Millipeds  
Sow bugs  
Carabid beetles } Taken only when other foods  
                          } are not available and then with  
                          } noticeable distaste.  
Meal worms (*Tenebrio molitor* larvae)  
Cockroaches  
Flies  
Termites

##### Plant food:

Dandelion heads: Both floral liques and winged  
fruits taken.  
Grass blades

Under natural conditions considerable sand is ingested in feeding. The stomach contents of most individuals obtained in the field possessed many sand particles.

Further, the stomachs of 10 animals examined possessed nematode worms. Unparasitized individuals possibly become infected by feeding on tenebrionid beetles which form a large part of the diet. These insects are scavengers and are known to be scatophagous. They may feed on the fecal masses of *Uma*. The fecal pellets of infected *Uma* would contain the nematode eggs. However, the worms have not as yet been looked for in these insects.

#### SELECTION OF PLACES OF RETREAT

##### RODENT BURROWS

*Uma* is physically equipped for, and capable of making, excavations for retreat, yet in nature burrows are seldom constructed. I have often watched captive animals in their attempt to dig out of their

places of confinement. The soil is scraped to one side and backward by rapid successive strokes given with one forelimb and then a series executed with the other. The heaped-up sand is pushed backwards with the hind limbs. In the loose soil of the habitat the slumping of sand into the burrow makes its maintenance difficult, but the capacity for digging is present. Furthermore, *Dipodomys* is able to maintain burrows in the same environment.

Probably an explanation for the failure on the part of *Uma* to construct tunnels for retreat while at the same time and in the same region burrows are maintained by certain desert rodents, lies in the different periods of activity of the animals. *Uma* is active during times of the year when the sand is dry and loose, such as in the spring, early summer, and fall. At such times, the establishment of a tunnel would mean the removal of tremendous amounts of sand in order to reach the more compacted layers which would support a burrow. The rodents, on the other hand, are active through a greater part of the year, including the winter months. There are many opportunities for tunnel construction because of the cementing of the surface layers associated with sporadic winter and spring precipitation. Once the burrow is established its maintenance requires comparatively little expenditure of energy.

Thus *Uma* rarely is found excavating cavities in the sand except following rains. Rather, the lizards make use of the rodent burrows, which are common features of the aeolian habitat.

#### SAND-SWIMMING

Retreat more frequently takes the form of sand-swimming, except for the very young individuals which seem to prefer ready-made cavities about the periphery of the deeper loose deposits. However, the juvenals soon adopt the habits of the adults.

Where barehans, dunes, or hummocks abound, the lizards are seldom uncovered on the windward side but rather occur more commonly toward the base of the more precipitous lee side of such deposits. This behavior prevents the excavation of the buried animals by wind action. Cowles (1941) points out that during relatively long periods of submergence, such as during hibernation or aestivation, such behavior would result in deep burial by wind-blown sand unless locomotory adjustments are made. Such movements of accommodation to changing depth of overlying sand have not been directly observed, but they are suggested by the location of captive hibernating individuals.

Knowledge of this behavior in *Uma* has led to the development of an effective collecting technique. Noosing of the animals is a slow process based upon capture of individuals startled from the sand or of those which happened to be on the surface and which remain there. The procedure is as follows: A rake is employed to move quantities of sand along the lee side of dunes, hummocks, and other elevations. Raking is begun at the base of the deposit, and re-

moval of the sand causes a downward slumping of sand. Slowly the level of the face of the accumulation is lowered. Buried animals are gradually exposed in this way and are easily captured, ordinarily not taking flight until well uncovered.

The west face of the sand heaps often provides the best morning collecting since the animals gather and finally submerge on the sunny side of the hummocks with the evening temperature decline.

Startled animals frequently seek cover beneath bushes, hiding in the shadows or submerging into the sand beneath the branches. I have often been baffled by my inability to find an individual which had disappeared into a bush, even when there was no indication from tracks that the shelter had been abandoned. In many such cases the bush, if isolated and small enough, was uprooted and the sand carefully sifted through the fingers, with negative results. Recently the discovery of several specimens under such conditions has provided an explanation which probably applies to some of the previous failures. In these cases the lizards were found buried a few inches beyond the side of the bush opposite the place of entrance. This behavior, if a constant one, may be of value in eluding enemies.

Although *Uma* often enters the sand facing in the same general direction as that assumed during surface locomotion, when alarmed both captive and field animals usually execute a sharp turn from the general course of movement in submerging into the soil. Such behavior probably is of distinct survival value in baffling predators (Fig. 21).

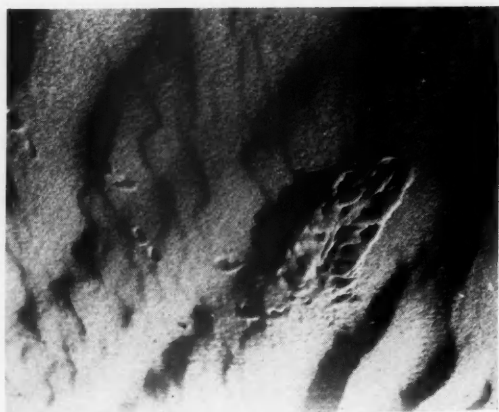


FIG. 21. *Uma notata notata* incompletely submerged following escape from a badger which had dug into its hiding place. Partial submergence was due to low temperatures. Note from its tracks that the lizard turned at almost a right angle to dive into the sand. (Photo by R. B. Cowles.)

#### ENEMIES

Little definite information has been obtained as to the animals which prey upon *Uma*. However, the road-runner (*Geococcyx californianus*) and the badger (*Taxidea taxus berlandieri*) have been definitely estab-

lished as predators. The shrike (*Lanius ludovicianus gambeli*), the sparrow hawk (*Falco sparverius phalaena*) and among the snakes, the sidewinder (*Crotalus cerastes*) and the western glossy snake (*Arizona elegans occidentalis*) are probable enemies.

Road-runner tracks are common on the dunes and by their location suggest that these birds search for *Uma*. Road-runners have been observed to feed on the lizards.



FIG. 22. Excavation made by a badger (*Taxidea taxus berlandieri*) in an effort to capture a buried lizard. In this case, the lizard escaped. Its tracks were followed from the badger workings to the top of the dune where it was found partially submerged (Fig. 21). (Photo by R. B. Cowles.)

Figure 22 shows the excavation made by a badger on the flank of a dune, in its attempt to uncover a buried lizard. In this instance the prey escaped and its track was followed, leading from the badger serapings up onto the top of the dune. In this location, the lizard was found half buried. Low temperatures are associated here with incomplete submergence (Fig. 21).

The shrike is a common predatory bird occurring in the habitat occupied by *Uma*. It is known to take lizards. Sparrow hawks have been observed hovering over the dunes. These birds probably capture many of the animals.

The two snakes mentioned frequent most areas occupied by the *Uma*. Both species may feed on the lizards.

#### THERMAL TOLERANCE

Cowles (*in litt*) provided the following data on temperature. The minimum voluntary tolerance for *Uma* is 26° C. The average of the normal activity range, or optimum temperature is 38.3° C. 40° C. is the maximum observable voluntary tolerance and 45° C. the critical maximum. Lizards subjected to temperatures of 45° C. or higher are incapacitated. Under field conditions, this may be considered the lethal temperature. In the laboratory, such animals may be cooled and revived.

Temperature exerts a most profound effect on the activities of these animals. Deleterious fluctuations

are adjusted to by sand-swimming, retreat to bushes or to rodent burrows.

Since the surface of the exposed sand of the habitat may reach temperatures well above the critical maximum, cover is indispensable. Mosauer (1935) records surface temperatures from 50-60° C. at noon in April and June on the top of dunes in the Coahuila Valley.

#### SUMMARY

The saurian genus *Uma* of the southwestern United States and northern Mexico comprises three species, *Uma inornata*, *U. notata notata*, *U. scoparia* and one subspecies *U. notata cowlesi*. These lizards characteristically occupy areas of loose aeolian sand. The habitat is one of extreme aridity and is typically sparsely vegetated.

Retreat from enemies and deleterious temperatures is accomplished by sand-swimming. This behavior implies submergence into the sand by wriggling rather than by burrow or tunnel construction.

The lizards possess numerous adaptations which facilitate existence under the adverse conditions of their environment. A brief survey of some of these adaptative modifications follows:

##### *Eyelids and nictitating membrane*

The free edges of the eyelids overlap, an arrangement which tends to prevent the incursion of sand particles during sand-swimming. The lids come together along an outer and an inner ridge, a chamber occurring between them. The double occlusion of the lids tends to prevent loss of water from the eye. If sand particles were to reach the moist inner contacting ridges, fluid would be removed from the orbital region by capillary action. Perception of changes in light intensity may be possible through a translucent area in the lower eyelid.

Sand which reaches the eye surface either by wind action or through sand-swimming, accumulates in the anterior eye corner. This sand becomes encapsulated in mucous and is expelled by the action of the nictitating membrane.

##### *Pineal eye*

On the basis of the external appearance of the pineal organ and certain of the habits of the lizards, the parietal eye was thought to have functional possibilities, but anatomical studies and experimental procedures failed to support this conjecture.

##### *Hearing*

Hearing has been clearly established for *Uma*. The lizards not only detect sounds such as whistled notes, snapping of fingers, and talking but also, even when buried, those produced by the movements of insect prey on the surface of the sand.

##### *Locomotion*

Surface locomotion is facilitated by elongated toes, the surfaces of which are increased by the presence of lateral digital fringe-scales. The gait is largely bipedal during rapid movement over the sand.

Most fossorial activity appears to be limited to movements not over several times the total length of the animal. Sand-swimming is accomplished by lateral movements of the head and fore parts, accompanied by propulsive movements of the hind feet. The forelimbs are not employed in submergence but lie appressed to the sides. The action of the hind foot and fringes is valvular.

#### Camouflage

The color of the lizards approximates that of the sand upon which they dwell. Cast shadow is frequently concealed by lying close to the ground. Spots and streaks in the eye region, arranged essentially in a linear series, tend to mask the eye in most individuals. The eye pattern is particularly effective when the lizards lie among the intricate shadow of bushes.

#### Feeding habits

Sight is most frequently used in the detection of food. Hearing and smell may also be employed.

Both animal and plant foods are taken, insects predominating in the diet. Tenebrionid beetles are an important item, at least at certain times of the year with the lizards in the Garnet habitat of the Coachella Valley, California.

#### Selection of places of retreat

Retreat from enemies and deleterious temperatures is usually accomplished by sand-swimming. Rodent burrows and other excavations are often used also.

The lizards tend to bury themselves on the lee side of dunes and hummocks to avoid excavation by prevailing winds.

#### Enemies

The road-runner (*Geococcyx californianus*) and badger (*Taxidea taxus berlandieri*) have been incriminated definitely as predators on *Uma*. The butcher bird (*Lanius ludovicianus*), the desert sparrow hawk (*Falco sparverius phalaena*) and among reptiles, the sidewinder (*Crotalus cerastes*) and the western glossy snake (*Arizona elegans occidentalis*), are probable enemies.

#### Thermal tolerance

Minimum voluntary—26° C.

Average of normal activity range—38.3° C.

Maximum observable voluntary tolerance—40° C.

Critical maximum—45° C.

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THE FATE OF ANIMALS IN STREAM DRIFT  
WHEN CARRIED INTO LAKES

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# THE FATE OF ANIMALS IN STREAM DRIFT WHEN CARRIED INTO LAKES

## INTRODUCTION

This paper deals with the fate of macroscopic aquatic animals occurring in stream drift when streams carry them into lakes. The fate of animals removed, by natural agencies, from their usual surroundings into a new environment is a matter of considerable biological interest. Chandler (1937) found that typical lake plankton, suddenly subjected to stream conditions, underwent a quantitative decrease as it passed downstream. In the present investigation the reverse situation existed, since the organisms usually able to maintain their positions in the creek, were swept downstream and into the lake by the force of the current.

The presence of aquatic animals in stream drift is well known. The occurrence of stream animals drifting in floods was reported by Needham (1929) and Beauchamp (1932). Moffet (1936) found that certain creek bottoms were barren after floods, and that the eroded areas became repopulated from uneroded tributaries. This repopulation was attributed to the tendency for organisms or their eggs to drift downstream before their final attachment. Leonard (1942), when experimenting with newly excavated stream-channel diversions, observed a rapid influx of bottom organisms into the newly created habitat. He concluded that the organisms invading the new habitat must have drifted into the area from upstream, either as eggs or as nymphs and larvae. The animals drifting in streams during absence of floods have attracted comparatively little attention. Needham (1928) found, during studies of "drift food" in relation to trout, that only 6.98 percent, by weight, of the animals was aquatic in origin, the rest was terrestrial. Ide (1942), when studying the availability of aquatic insects as food of the speckled trout, classified drift material as aquatic, emerging, exuviae, aerial, and lacustrine.

Up to the present time no intensive study has been devoted to the stream organisms which occur in drift in streams not subject to floods. Needham (1930) found that pools serve as catch basins for animals which are swept down from riffles. Apparently study of the fate of these organisms, when washed into lakes, has hitherto been entirely neglected.

In this investigation work was done where floods or even freshets are absent. The stream drift consisted of particles of debris, mostly macroscopic in size, and various animals, either living or dead.

The writer wishes to express his indebtedness to Professor Paul S. Welch, under whose direction this work was done; to Dr. W. K. Townes for identification of Chironomidae; to Dr. H. H. Ross for identification of Trichoptera; to Dr. F. Earle Lyman for identification of Ephemeroptera; and to Professor C. W. Creaser for identification of fishes.

## SITUATIONS STUDIED

In planning this investigation the writer was faced with two alternatives: (1) to study several situations, or (2) to restrict the work to an intensive study of one. The former was impracticable because of the amount of time consumed in reaching the widely separated available places. The latter was chosen because it was deemed more desirable to study in detail one situation ideal for this problem than to spread effort and time on what could only have been a survey. Hence, most of the work was confined to Carp Creek.

Carp Creek is on the University of Michigan Biological Station tract, Cheboygan County, Michigan, and flows from High Springs, about 0.5 mile south of Douglas Lake, into Burt Lake, a distance of approximately 1.5 miles. A stream built to order could hardly have been more perfectly suited to the purpose at hand. For this reason it seemed far more profitable to devote attention to Carp Creek and Burt Lake than to work on less suitable locations. The ideal features offered by this situation were as follows: (1) constancy of water flowage and consequent lack of floods or great changes in water level, (2) freedom from contamination, (3) absence of tributaries, (4) remarkably constant temperature throughout the stream, (5) little seasonal fluctuation of temperature, (6) lack of ice cover in winter, (7) unusual degree of uniformity of gradient, (8) uninterrupted current and lack of pools in which drift organisms might collect, (9) similarity of bottom materials in all parts of the stream, (10) abundance of fallen trees and brush in the stream, (11) presence of rooted aquatic vegetation, (12) abundant and diversified population of stream animals, (13) constant occurrence of animals in stream drift, (14) similarity of stream and lake bottom materials, (15) dissimilarity of creek and lake animals, (16) great extent of shallow water in the lake, allowing drift animals to settle to the bottom before reaching deeper water, (17) essential chemical likeness of the waters of the stream and lake, (18) great thermal differences between creek and lake during this investigation, allowing positive tracing of spread of creek water in the lake, (19) abrupt entry of the creek into the lake with little diminution of current at the mouth, (20) variety of lake conditions produced by protection of this area from north winds and exposure to heavy wave action of storms from the south, (21) existence of almost completely natural conditions, and (22) accessibility of the stream throughout its entire length. Stations were selected as follows (Figs. 1 and 2): Station 1, about 100 meters downstream from High Springs area; Station 2, a few meters downstream from the iron bridge about 1 mile from Burt Lake; Station 3, near an old

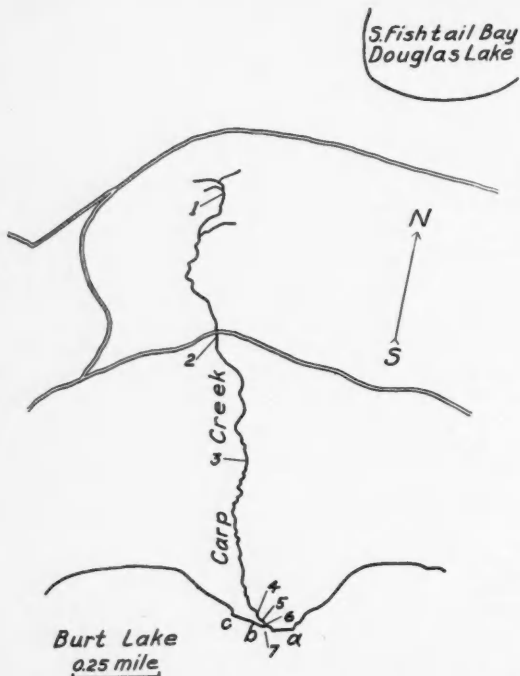


FIG. 1. Map of Carp Creek showing its position in relation to Burt Lake and South Fishtail Bay of Douglas Lake, Cheboygan County, Michigan. Collecting stations in the creek are indicated by Arabic numerals and experiment stations in the lake by lower case letters.

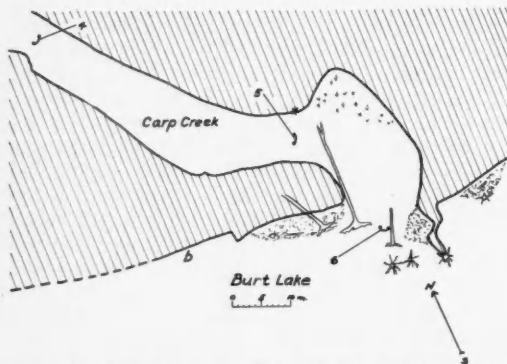


FIG. 2. Map of mouth of Carp Creek and immediate vicinity. Collecting stations in the creek are indicated by Arabic numerals and an experiment station in the lake by lower case letter "b."

beaver pond a few hundred meters farther downstream; Station 4, about 85 meters upstream from the mouth of the creek; Station 5, about 25 meters upstream from the mouth; and Station 6, at the mouth. The position chosen for Station 7 varied somewhat, but was lakeward from the mouth and in the direction of flow of Carp Creek water, usually 10 meters or more from shore. Sixty-five drift sam-

ples were taken in Carp Creek, most of them from Stations 4, 5, 6, and 7.

The region where Carp Creek enters Burt Lake was chosen for studying the fate of drift animals. In this vicinity 201 bottom samples and 17 collections of animals found on beaches were obtained. Field data and collections were taken during the summers of 1939, 1940, 1941, and 1942.

Drift samples from two additional streams supplied information for comparison of Carp Creek with other situations. The East Branch of Maple River, the outlet of Douglas Lake, after a somewhat circuitous route joins the West Branch and empties into Burt Lake. Station 8 was on the East Branch of Maple River in Emmet County, about 15 meters upstream from the bridge on the road extending east from Pellston, at the lower end of a riffle about 4 meters long. Fourteen drift samples were taken in the summers of 1939 and 1940, during which period the stream was about 3 meters wide and varied in depth from approximately 30 centimeters in June to only about 20 centimeters in late August or early September.

Station 9, in the West Branch of Maple River, was 3.5 miles northwest of Pellston. The West Branch, which is the outlet of Larks Lake, flows in a southeasterly direction, joining the East Branch about 2 miles southeast of Pellston. There was considerable current, but there were no riffles within about 10 meters. In June, 1939 and 1940, the stream was about 3 meters wide and approximately 70 centimeters deep; by the end of the summer about 55 centimeters deep. Twelve drift samples were taken here in the summers of 1939 and 1940.

## METHODS AND EQUIPMENT

The drift net described by Needham (1928a) was considered impracticable for use in Carp Creek because of the amount of debris in this stream. It was thought more desirable to secure numerous small samples from several stations than to study larger ones and restrict the number of samples.

Samples of stream drift were obtained by means of a net consisting of a rectangular piece of ordinary No. 16 (6.3 meshes per centimeter) wire screen 1.9 meters long and 0.76 meter high. The top and bottom selvages were strengthened by soldering small copper cables to them. Each end of the net was securely tacked to a staff extending 8 centimeters above and below the screen. It was installed in the stream by attaching it to two heavy stakes driven in the stream bottom about 2 meters apart on a line transverse to the current. To these stakes the net was attached by four small wire hoops, each of which encircled a stake and the top or the bottom of one of the staffs. The staffs were then pushed down until the lower edge of the screen made contact with the bottom. After about 1 hour the net, with the materials collected on it, was carefully lifted out of the water. The sample was washed off into a tub, concentrated in a cloth net, and transferred to a

bottle. The animals were separated from the debris in white pans. When practicable, sorting was done immediately in the field, while the animals were alive. Many of the samples were taken to the laboratory and kept alive in cold storage until they could be worked. The animals were preserved in alcohol.

In collecting bottom samples the Petersen dredge was used at first, but in places the animals were so abundant that it seemed profitable to reduce the area of each sample and thus be able to increase the number and spread of samples. Accordingly a smaller inverting sampler was devised. It consisted of a brass cylinder 7.8 centimeters in diameter and 13 centimeters long. The top end was covered with a piece of brass gauze (about 9 meshes per centimeter). A handle frame (Fig. 3) was attached to the top of

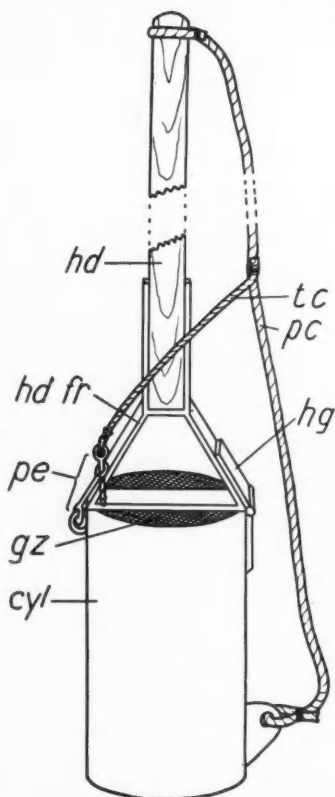


Fig. 3. Bottom sampler with cylinder set in position for sampling. cyl, Cylinder; gz, brass gauze; hd, handle; hd fr, handle frame; hg, hinge; p e, pin-and-eye fastener; t c, trip cord.

the cylinder by a hinge on one side and by a pin-and-eye fastener on the other. A wooden handle was fitted into the frame, and a pull cord connected from the top of the handle to bottom of the cylinder on the hinge side. A trip cord extended from the pin to the pull cord, being so adjusted that tightening the pull cord released the fastener and inverted the

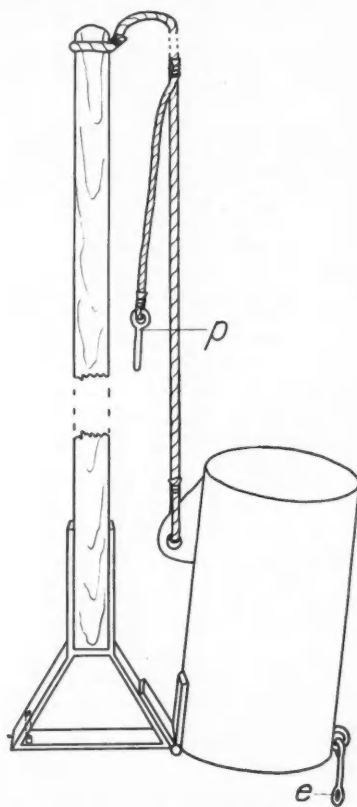


Fig. 4. Bottom sampler with cylinder in the inverted position. Symbols as in Figure 3.

cylinder (Fig. 4). To obtain a sample the cylinder was fastened in place (Fig. 3) and pushed into the stream or lake bottom about 10 centimeters. While continuing to push the sampler down the operator inverted the cylinder by pulling the cord. The sampler was then lifted out of the water and its contents dumped into a circular sieve. All residue in the sampler was washed into the sieve. The sample was screened, concentrated, and placed in a bottle. Sorting and preservation of bottom animals was done in the manner described for drift samples.

A map of the mouth of the creek and the surrounding area, within a radius of about 60 meters (Fig. 2), was made by means of a plane table.

Lowering of the surface level of Burt Lake was recorded roughly by cutting notches in the sides of some stumps along the shore and measuring the vertical distances between notches and surface of the water.

Chemical analyses were done by the methods outlined in Standard Methods for Examination of Water and Sewage, eighth edition (1936). Temperatures were measured by maximum-minimum thermometers and by the thermophone. The latter was employed in tracing the spread of creek water in the lake.

## DRIFT DATA

During this investigation drift samples from Carp Creek and the two branches of Maple River contained 71 kinds of animals from the phyla: Coelenterata, Platyhelminthes, Nematomorpha, Nematoda, Annelida, Mollusca, Arthropoda, and Chordata. Table 1 presents a list of the drift organisms collected in the three streams and supplies the following data for each kind of animal in each stream: (1) the percentage of samples in which the animal occurred, (2) the total number of individuals collected, and (3) the variation of numbers of individuals per sample. The total number of individuals and the variation per sample give a general idea of the relative abundance of each form. Because of the presence of several variables such as (1) rate of flow of water screened, (2) depth of water, (3) change of screening efficiency due to the clogging effect of debris on the drift net, and (4) length of time the net was in the water, this study cannot be considered as quantitative. This study was not of a taxonomic nature. Although the writer acknowledges the desirability of having complete identifications for all organisms concerned, due to the wide variety of types of animals and stages of development it seemed impracticable to attempt identification, beyond major groups, of any individuals except those which seemed to be of considerable importance to the problem in hand.

By comparison of the data shown in Table 1 it is readily seen that drift samples from these three streams show certain conspicuous differences: for instance *Gammarus limnaeus* and *Asellus communis* were found only in Carp Creek, while *Hyalella azteca* (*knickerbockeri*) occurred only in the West Branch of Maple River. Although *Baetis* was found in all three streams, Dr. F. Earle Lyman informed the writer (personal communication) that the species present in Carp Creek was *Baetis brunneicolor* McDunnough, but that specimens from the two branches of Maple River probably represent other species. The plecopteran, *Nemoura venosa*, was common in Carp Creek, but absent from the other streams. Some small fishes were taken in Carp Creek, and a few individuals of Corixidae occurred in samples from the West Branch of Maple River, but as these animals are active swimmers their inclusion as animals of the stream drift would be questionable. Among the Trichoptera some larvae of Brachycentrinae, probably *Brachycentrus americanus*, occurred in 28 drift samples from Carp Creek and totalled 1,045 individuals, in contrast to 4 occurrences of single specimens in the East Branch of Maple River and one in the West Branch. The greatest abundance of Brachycentrinae occurred during July and August 1940, and apparently was in some way connected with a life history stage. Hundreds of them drifted downstream and were washed ashore near the mouth of the creek, where they were seen clinging to the masses of roots and brush at the edge of the lake. In 1941 similar trichopterous larvae hung on objects in the stream, but not in such abundance as in 1940.

Occasionally pieces of Potamogeton and other aquatic plants, or twigs which had been submerged in the current, drifted into the net. Such an occurrence almost always brought many larval Simuliidae attached to these plants. Usually they were so numerous that no attempt was made to count them. Larvae of aquatic Lepidoptera were present in collections from the West Branch of Maple River, but absent from those in the other two streams.

The considerable numbers of terrestrial animals, mostly insects, which were in the drift samples have not been considered in this investigation.

On July 23, 1940, a drift sample at Station 3 contained 107 very small mayfly naiads, apparently *Baetis*, though the practicability of identification of such early instars was doubtful. These animals could have passed through the meshes of the drift net with ease. It seems that they were caught partly because they clung to the net and partly because the accumulating debris on the net reduced the effectiveness of the straining. It is likely that many such animals were not captured but passed directly through the meshes of the net.

Frequently clusters of eggs in masses of jelly occurred in drift samples. Usually identification of these eggs was impracticable. A thorough study of the eggs present in stream drift would undoubtedly show interesting facts concerning the relation of drift to the distribution of stream animals and the repopulation of erosion areas, such as those mentioned by Moffett (*loc. cit.*).

Representatives of all species of macroscopic animals collected from Carp Creek bottom, except Pentaneura and Procladius, were sooner or later found in drift samples. The fact that individuals of a certain species were relatively numerous in bottom samples did not necessarily mean that they would be abundant in the drift samples. Active animals, such as *Gammarus limnaeus*, were more apt to drift than chironomid larvae which inhabit sand cases. Certain animals, Simuliidae, *Brachycentrus americanus*, and other Hydropsychinae, which normally remain firmly attached to stationary objects in the stream, occurred in stream drift. Black-fly larvae frequently occurred in drift samples. Needham (1929) stated that black-fly larvae (*Simulium*) were not taken in drift under ordinary circumstances, but were present in samples collected during a flood. Data from drift samples in Carp Creek and the two branches of Maple River furnish evidence that these larvae are not exempt from being carried away in ordinary stream current.

The condition of the animals in the drift varied greatly. Most of the individuals seemed vigorous and in excellent state; but others were parasitized, had failed to complete ecdysis, had legs missing, or in some way showed low vitality. Dead animals, especially mayflies and chironomids which had died when only partially emerged, frequently occurred in samples.

It was interesting indeed to note the large number of larval and pupal exuviae which were present in



TABLE 1. Summary of drift data. Comparison of the occurrences of animals in drift from three streams. Numbers under Percent indicate percentage of samples in which the kind of animal occurred; those under Total refer to the total number of individuals collected; and those under Number show the variation of numbers of individuals per sample. Samples were collected during summers of 1939, 1940, and 1941. Insects are larval except when otherwise indicated.

	63 samples from Carp Creek			14 samples from East Branch of Maple River			13 samples from West Branch of Maple River		
	Percent	Total	Number	Percent	Total	Number	Percent	Total	Number
Hydra.....	3	2	1				15	5	1-4
Turbellaria.....				14	4	2	15	3	1-2
Cestoda.....							7	1	1
Nematoda.....	3	2	1						
Gordius (?).....	3	2	1	21	5	1-2	7	1	1
Oligochaeta.....	22	99	1-34				31	9	1-4
Gastropoda.....	15	18	1-5	21	3	1	69	25	1-6
Sphaeriidae.....	16	19	1-5	7	1	1			
<i>Asellus communis</i> Say.....	30	33	1-11						
<i>Gammarus linnaeus</i> Smith.....	86	689	1-45						
<i>Hyalella azteca</i> (Saussure).....							69	48	1-20
<i>Stenonema</i> sp.....				71	20	1-4	7	1	1
<i>Blasturus</i> sp.....	2	2	2	7	1	1			
<i>Tricorythodes</i> sp.....				43	13	1-4			
<i>Caenis</i> sp.....				14	4	1-3	38	6	1-2
<i>Baetis</i> spp.....	86	540	1-107	43	37	1-16	23	13	1-10
<i>Ephemerella</i> sp.....				21	24	2-20			
<i>Pseudocloeon</i> sp.....				7	1	1	15	9	3-6
<i>Chauliodes</i> sp.....				7	1	1			
Anisoptera.....	6	4	1	14	5	1-4			
<i>Agriion</i> sp.....				28	4	1	38	8	1-4
Pteronarcidae.....				7	1	1			
<i>Nemoura venosa</i> Banks.....	60	100	1-10						
Halipidae (adult).....	19	13	1-2	7	1	1			
Halipidae.....				28	4	1	23	5	1-2
Dytiscidae (adult).....	25	23	1-6	21	4	1-2			
Dytiscidae.....	3	2	1						
Hydrophilidae (adult).....	15	14	1-5	43	25	1-10	7	1	1
Hydrophilidae.....				14	3	1-2	15	2	1
Dasyllidae.....				28	16	1-8			
Glossomatinae (?).....	2	1	1	7	1	1			
Hydroptilidae.....	2	2	2				15	3	1-2
Philopotamidae.....	2	1	1	7	1	1			
Hydropsychinae.....	6	5	1-2	100	135	1-11	38	7	1-2
<i>Brachycentrus americanus</i> (Banks).....	44	1,045	1-112	28	4	1			
Sericostomatidae.....	8	5	1						
Leptoceridae.....				43	10	1-3	85	185	1-39
Phryganeidae.....	15	17	1-4				7	1	1
Limnephilidae.....	37	58	1-9	36	7	1-2	38	34	1-30
Polycentropidae.....							7	1	1
Psychomyidae.....				7	1	1			
Lepidostomatinae.....				7	1	1			
<i>Nymphula</i> sp.....							38	18	1-8
<i>Paraponyx</i> sp.....							46	9	1-2
Tipulidae.....	5	3	1	7	1	1			
Ptychopteridae.....									
<i>Pentaneura</i> sp.....				21	6	1-3	7	1	1
<i>Procladius</i> sp.....				7	1	1	69	28	1-6
<i>Procladius</i> sp.....							7	1	1
<i>Procladius</i> sp.....	16	12	1-2						
<i>Corynoneura</i> sp.....	46	535	1-145	36	9	1-3	92	19	1-3
<i>Trichocladius</i> n. sp.....	5	8	2-4						
Orthocladinae.....	71	651	1-64	71	158	1-46	92	306	7-51
<i>Tanytarsus confusus</i> Mall. (?).....	60	107	1-14	50	21	1-5	62	29	1-12
<i>Tanytarsus gregarius</i> Kieffer (?).....				28	31	4-13	46	69	2-29
<i>Tanytarsus</i> sp.....				21	27	1-20	38	14	1-5
<i>Chironomus (Harnischia)</i> sp.....	27	38	1-6						
<i>Chironomus aberrans</i> Joh. (?).....				7	4	4	23	5	1-2
<i>Chironomus</i> (?) (on <i>Chauliodes</i> ) sp.....				7	2	2			
<i>Polypedium flavus</i> Joh. (?).....				93	202	1-56	69	67	2-40
<i>Endochironomus</i> sp.....	21	38	1-18						
<i>Cryptochironomus</i> n. sp.....				14	2	1			
<i>Cryptochironomus</i> sp.....	3	5	1-4	21	3	1	7	1	1
Chironomidae (pupa).....	46	102	1-56	28	15	2-5	38	7	1-2
Simuliidae.....	62	142	1-21	93	10,000	1-4,000	100	88	1-124
Empididae.....	3	2	1	7	1	1	7	1	1
Rhagionidae.....	3	2	1						
Ceratopogonidae.....							15	2	1
Stratiomyidae.....	2	1	1						
Anthomyidae.....	2	1	1						
Hydracarina.....	32	36	1-7				54	13	1-6
Anura (larva).....	8	13	1-9						

the stream drift. Many of these were intact and could be identified with comparative ease. Frequently structural features were much easier to determine from exuviae than from larvae themselves. Ide (*loc. cit.*) found that exuviae constituted 56.1 percent, by volume, of the drift.

Except for representatives of *Blasturus* and *Hydroptilidae*, each of which occurred in only one sample, all species of animals found at Stations 1, 2, and 3 were found near the mouth of the creek in drift and bottom samples. Apparently the major portion of the drift material in Carp Creek was carried into Burt Lake.

In order to determine how far stream animals were carried into the lake before they settled to the bottom, attempts were made to procure drift samples in the creek current at varying distances lake-ward from shore. Stream drift was obtained only during periods when the lake was very calm in that area. A drift net installed 10-30 meters from the mouth of the creek or the edge of the delta collected a little drift material while calm lasted. The onset of a breeze after a short while often caused waves which washed the catch from the net. Few stream animals occurred in drift samples as far as 30 meters from the mouth of the stream. Only two of the 10 or more samples at that distance from shore contained creek species. One of these samples was collected in 1940 and the other in 1941. When any appreciable wave action was present in this region, obtaining samples of stream drift beyond 10 meters from the delta at the mouth of the creek was quite impracticable because of the fact that the waves almost invariably washed the catch from the net.

Because of the great degree of variation in drift samples collected in the creek current in Burt Lake, this method of study yielded little information concerning the fate of stream animals in the lake, except that practically all of them appeared to settle to the bottom less than 30 meters from the delta. Because of this settling it was thought that a study of distribution of animals on Burt Lake bottom in the area near the mouth of the creek would yield desirable information.

Studies of drift samples showed the following: (1) animals from the bottom and margins of Carp Creek were constantly present in the drift; (2) their occurrence must be considered as an entirely normal circumstance, at least during the summer months, for this stream is not subject to floods or sudden changes in water level which might dislodge the animals from their homes; (3) in the course of a summer stream animals in vast numbers must therefore be washed out of the creek into Burt Lake. During this investigation no outstanding instances of seasonal differences in drift populations were apparent except in the cases of *Baetis* and *Brachycentrus* mentioned heretofore. On the basis of such work as was done there was thought to be no occasion to go into seasonal variations exhaustively.

## ANIMALS OF STREAM BOTTOM

In order to ascertain the distribution of creek animals in Burt Lake it was necessary to determine what animals were typical of Carp Creek. Bottom samples were collected with the inverting sampler from various parts of the stream, especially in the region within 85 meters of the mouth. The stream animals of special interest, since they occurred in drift samples as well as bottom samples, were as follows: *Nematoda*, *Oligochaeta*, *Sphaeriidae*, *Asellus communis*, *Gammarus limnaeus*, *Baetis brunneicolor*, *Nemoura venosa*, *Brachycentrus americanus*, *Prodiamesa* sp., *Orthocladiinae*, *Trichocladus* n. sp., *Tanytarsus confusus* (?), *Tanytarsus* sp., *Chironomus* (*Harnischia* ?) sp., *Endochironomus* sp., *Cryptochironomus* sp., *Chironomus* (?), some pupae of *Chironomidae*, and larvae of *Ceratopogonidae*. Though specimens of *Brachycentrus americanus* were rarely collected in bottom samples because of their

TABLE 2. Summary of data from bottom samples. Numbers refer to percentage of samples in which the kind of animal occurred. Data are from 24 samples collected in the creek, definitely upstream from the mouth, and 20 samples from areas in Burt Lake not in the vicinity of Carp Creek. Samples were obtained during summers of 1940 and 1941.

	Creek samples percent	Lake samples percent
<b>Animals in the creek:</b>		
<i>Asellus communis</i> .....	16	..
<i>Gammarus limnaeus</i> .....	50	..
<i>Baetis brunneicolor</i> .....	16	..
<i>Nemoura venosa</i> .....	4	..
<i>Brachycentrus americanus</i> .....	4	..
<i>Pentaneura</i> sp.....	4	..
<i>Procladius</i> sp.....	16	..
<i>Prodiamesa</i> sp.....	79	..
<i>Corynoneura</i> sp.....	4	..
<i>Trichocladus</i> n. sp.....	50	..
<i>Tanytarsus confusus</i> (?).....	62	..
<i>Rhagionidae</i> .....	21	..
<b>Animals in creek and lake:</b>		
<i>Nematoda</i> .....	4	10
<i>Oligochaeta</i> .....	37	55
<i>Sphaeriidae</i> .....	29	5
<i>Orthocladiinae</i> .....	62	10
<i>Tanytarsus</i> sp.....	4	30
<i>Endochironomus</i> sp.....	83	15
<i>Chironomus</i> ( <i>Harnischia</i> ?) sp.....	62	5
<i>Cryptochironomus</i> sp.....	37	5
<i>Chironomus</i> (?) sp.....	12	5
<i>Chironomidae</i> (pupa).....	33	10
<i>Ceratopogonidae</i> .....	8	30
<b>Animals in the lake:</b>		
<i>Hirudinea</i> .....	..	15
<i>Gastropoda</i> .....	..	10
<i>Hyalella azteca</i> .....	..	15
<i>Ephemeroptera</i> spp.....	..	5
<i>Tanypodinae</i> .....	..	20
<i>Tanytarsus gregarius</i> (?).....	..	25
<i>Polyptilum flavus</i> (?).....	..	15
<i>Cryptochironomus</i> n. sp.....	..	35
<i>Pseudochironomus</i> spp.....	..	30
<i>Chironomus</i> spp.....	..	5
<i>Hydracarina</i> .....	..	10

habit of clinging on logs, twigs, etc., they were common in drift samples.

By comparing bottom samples collected in portions of the lake distant from the creek with samples obtained in the stream (Table 2) it was seen that animals present in both environments included: Nematoda, Oligochaeta, Sphaeriidae, Orthocladinae, *Tanytarsus* sp., *Endochironomus* sp., *Chironomus* (*Harnischia* ?) sp., *Cryptochironomus* sp., *Chironomus* (?), some pupae of Chironomidae, and larvae of Ceratopogonidae. When animals of the former list not included in the latter one were found on Burt Lake bottom they could be identified as drift animals which originally were products of bottom or margin or the stream. The dispersal of these animals in Burt Lake was remarkably restricted.

Distributions of creek animals in the lake were plotted by spotting on a map the locations of samples in which they were collected. Four distribu-

tion areas are shown in Figure 5. This is not a complete discussion of total fauna, as the investigation concerns only the animals directly involved in stream drift. It is the opinion of the writer that regions indicated are amply large to include the entire spread of the creek animals named, except in cases of dispersal due to severe wind action which may have carried a few animals farther from the stream. However, since such animals probably could not survive wave action, the extended distribution would have been ephemeral in duration. Practically all the samples containing creek animals were within the area designated for Gammarus.

#### ABUNDANCE OF DIFFERENT KINDS OF ANIMALS

Bottom samples were collected in order to make a rough estimate of the abundance of different kinds of animals in the portion of Carp Creek within 27.5 meters from the mouth of the stream, and in the part of Burt Lake not more than 120 meters lakeward from the creek. Transects were made in the stream transverse to the current at distances of 10, 25, and 27.5 meters upstream from the lake. Several samples were obtained from the mouth of the creek. Lake bottom samples were collected at distances of 2.5, 5, 10, 20, 30, 35, 60, and 90-120 meters lakeward from the creek. The samples were collected between June 29 and August 9, 1940, during which time the delta progressed only a few meters lakeward from the mouth of the stream.

Data from these samples (Table 3) show that stream animals were abundant in samples from transects 10, 25, and 27.5 meters upstream from the mouth of the creek. Fewer organisms occurred at the mouth of the stream. Many creek animals were in samples from the transect 2.5 meters lakeward from the mouth of the stream. This transect was in

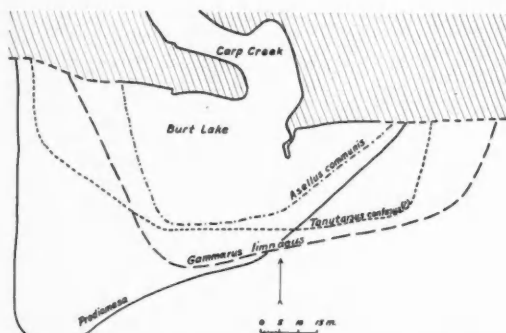


FIG. 5. Map of the mouth of Carp Creek and the immediate vicinity showing the lakeward limits of areas where certain drift animals were found on Burt Lake bottom.

TABLE 3. Distribution of creek and lake animals in the area near the mouth of Carp Creek. Data from bottom samples collected in summer of 1940. Numbers are averages of individuals per 100 square centimeters. Distance from mouth of creek and number of samples represented are listed at top of each column.

	27.5 meters upstream, 3 samples	25 meters upstream, 7 samples	10 meters upstream, 4 samples	Creek mouth, 8 samples	2.5 meters lakeward, 6 samples	5 meters lakeward, 4 samples	7.5 meters lakeward, 14 samples	10 meters lakeward, 4 samples	20 meters lakeward, 5 samples	30 meters lakeward, 4 samples	35 meters lakeward, 6 samples	60 meters lakeward, 7 samples	90-120 meters lakeward, 8 samples
<i>Gammarus limnaeus</i> .....	2.3	2.3	0.5	1.6	6.8	1.1	0.7	.....	0.9	.....	.....	.....	.....
Limnephilidae .....	.....	.....	.....	.....	2.0	0.5	.....	.....	.....	.....	.....	.....	.....
<i>Brachycentrus americanus</i> .....	.....	.....	.....	.....	.....	0.5	0.2	.....	.....	.....	.....	.....	.....
<i>Procladius</i> sp. ....	18.1	4.5	0.5	9.1	4.5	0.5	0.7	1.1	0.5	.....	.....	.....	0.2
<i>Trichocladius</i> n. sp. ....	27.2	3.8	9.1	1.6	1.6	0.5	.....	1.1	.....	0.5	.....	.....	0.2
<i>Tanytarsus confusus</i> (?) .....	615.7	65.6	163.0	19.2	88.5	28.3	63.4	31.7	11.3	.....	.....	.....	.....
<i>Endochironomus</i> sp. ....	219.6	34.0	81.5	18.1	28.7	1.1	7.0	3.8	8.1	9.1	.....	.....	.....
<i>Chironomus</i> ( <i>Harnischia</i> ?) sp. ....	11.3	3.6	1.6	1.1	2.3	1.6	0.9	1.1	2.7	1.1	.....	.....	.....
Oligochaeta .....	34.0	0.9	9.1	.....	.....	.....	0.5	.....	1.4	11.8	21.5	7.7	17.0
<i>Hyalella azteca</i> .....	.....	.....	.....	.....	.....	.....	.....	.....	.....	0.5	7.5	0.7	1.6
<i>Tanytarsus gregarius</i> (?) .....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	0.7	0.9
<i>Tanytarsus</i> sp. ....	.....	0.2	.....	.....	.....	.....	.....	.....	.....	.....	1.1	2.0	3.4
<i>Pseudochironomus</i> spp. ....	.....	.....	.....	.....	.....	.....	.....	.....	.....	2.3	2.3	0.2	.....
<i>Polypedilum flavus</i> (?) .....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	0.5	1.4	0.2
<i>Cryptochironomus</i> n. sp. ....	.....	.....	.....	.....	.....	.....	0.2	.....	1.8	1.6	0.5	2.0	2.0

a zone of concentration of debris and animals. Few creek organisms were located in the lake beyond 35 meters from the mouth of the stream and not many lake animals occurred nearer the stream than 30 meters from its mouth. The area between 30 and 35 meters lakeward from the creek seemed to be the locale of a transition between creek and lake populations. *Tanytarsus* sp., apparently a lake species, occasionally occurred in the creek along the margins near the mouth, where current was greatly reduced. Judging by the data in Table 3 the occurrence of the following species indicated to what extent creek animals drifted into the lake: *Gammarus limnaeus*, *Procladius* sp., *Trichocladius* n. sp., *Tanytarsus confusus* (?), *Endochironomus* sp., and *Chironomus* (*Harnischia* ?) sp. Additional samples not included in the table showed that *Endochironomus* occurred, though rarely, in regions of the lake apparently far beyond the influence of Carp Creek. Species typical of Burt Lake bottom in the general region of Carp Creek were the following: *Hyalella azteca*, *Tanytarsus gregarius* (?), *Tanytarsus* sp., *Pseudochironomus* sp., *Polypedium flavus* (?), *Cryptochironomus* n. sp. For reasons stated earlier the species of oligochaetes were not determined. Representatives of this group were much more common in the lake than in the stream. However, in certain samples from the creek these animals were abundant.

#### RELATIVE ABUNDANCE OF CREEK ANIMALS IN AREAS OF LAKE

In order to ascertain the relative number of creek animals per 100 square centimeters at the mouth of the stream and in the part of the lake in that vicinity, bottom samples were obtained from: (1) the delta at points a few meters upstream from its lakeward margin; (2) the zone within a few meters immediately lakeward from the delta; (3) the region farther lakeward, but not more than 70 meters from the mouth of the creek; and (4) points in Burt Lake at distances greater than 70 meters from the creek. Data from these samples are in Table 4.

All animals included in these counts for Table 4 were of species that occurred in the stream drift. The first three columns show that the number of animals per sample was highly variable. This is especially evident in the second column, which refers to the area immediately lakeward from the delta. The extremes 9.1-837.4 individuals per 100 square centimeters in 1940 were so great that determination of mean animals per sample was worthless. The population of the delta was strikingly low in comparison with that of the region immediately lakeward from the margin of the delta. The location of a zone of concentration of creek animals on the lake bottom was usually marked by a mass of debris. This debris was composed chiefly of bits of partially decayed plant material varying in length from about 2 millimeters to several centimeters. Such debris on the lake bottom frequently lay in a more or less continuous mass, one meter or more wide and several

TABLE 4. Relative abundance of creek animals in Burt Lake. Data from bottom samples in region of mouth of Carp Creek. Each number represents total creek animals per 100 square centimeters.

	Delta	Concentration zone	Dispersion area	Region beyond creek influence
1940	2.3	212.8	56.6	0.0
	0.0	108.6	74.7	0.0
	4.5	837.4	9.1	0.0
	18.1	337.3	11.3	0.0
	9.1	147.1	9.1	0.0
	11.3	158.4	0.0	0.0
	9.1	83.7	58.8	0.0
	2.3	86.0	36.2	0.0
	2.3	63.4	18.1	0.0
	6.8	140.3	15.8	0.0
	9.1	61.1	24.9	0.0
	...	9.1	58.8	0.0
	...	38.5	13.6	0.0
	...	176.5	6.8	0.0
	...	271.6	...	0.0
	...	47.5	...	2.3
	...	...	...	0.0
	...	...	...	0.0
	...	...	...	0.0
	...	...	...	0.0
	...	...	...	0.0
Average.	6.8	173.7	28.1	0.1
1941	21.1	63.2	50.5	8.4
	14.7	130.5	14.7	2.1
	0.0	115.8	12.6	0.0
	0.0	40.0	29.5	0.0
	2.1	27.4	37.9	0.0
	...	52.6	58.9	0.0
	...	44.2	29.5	0.0
	...	52.6	31.6	4.2
	...	52.6	35.8	2.1
	...	37.9	48.4	0.0
	...	94.7	21.1	0.0
	...	40.0	21.1	0.0
	...	42.1	12.6	0.0
	...	86.3	8.4	0.0
	...	21.1	12.6	0.0
	...	27.4	73.7	0.0
	...	31.6	14.7	...
	...	31.6	4.2	...
	...	...	80.0	...
	...	...	6.3	...
	...	...	4.2	...
	...	...	18.9	...
	...	...	10.1	...
	...	...	12.6	...
	...	...	10.1	...
	...	...	2.1	...
Average.	7.6	55.1	25.4	1.1

meters long, surrounding the lakeward edge of the delta. In the adjoining area, lakeward from this zone of concentration, creek animals were more dispersed.

Boundary between the concentration zone and the dispersion area was more or less arbitrarily set at 3-5 meters lakeward from the delta, depending on development and extent of the concentration zone. The dispersion area extended from the concentration zone to not over 70 meters lakeward from the mouth of the creek. Creek animals were rarely collected



beyond this area. Most of the organisms in this area occurred within a few meters of the concentration zone. Two individuals, one of *Trichocladus* n. sp. and one of *Chironomus* (*Harnischia* ?) sp., were found in Burt Lake more than 90 meters from the mouth of Carp Creek. Occurrences of these species, typical of the creek, so far out as that in Burt Lake were rare exceptions. The latter individual was collected from a point southwest of the creek in a region where cold creek water was on the lake bottom, thus possibly it was carried to this region as stream drift. However, the individual of *Trichocladus* n. sp. was collected about 400 meters east of the creek.

Among the data for 1941 some of the numbers represent transects made along the concentration zone and a few meters lakeward. In each case 5 bottom samples were obtained and the concentrates placed together. From the total number of animals the average number per sample was computed. The last four items in the second column and the last three in the third column are averages from such transects.

There were more animals per sample in the zones of concentration in the summer of 1940 than in that of 1941. This was at least partly because the surface level of Burt Lake was several centimeters lower during the latter than the former summer. With the fall of water level the delta progressed farther out into the lake and spread considerably. As the distance around the edge of the delta increased the concentration zone became longer. Thus if the same number of animals were present in the concentration zone during both summers a smaller number per unit would be expected in 1941. In addition wave action, which interfered with concentration of creek animals, was greater in the summer of 1941 than in the previous summer.

#### SPREAD OF CREEK WATER INTO LAKE

In order to determine whether or not the spread of Carp Creek water into Burt Lake had any influence on the fate of drift animals, the distribution of this water in the lake was studied. In midsummer the shallow water at the north end of Burt Lake was practically homothermous on all occasions, but the temperature varied on different dates, owing to meteorological conditions, from about 18°-27° Centigrade. The temperature of the creek water at the mouth was 11°-14° Centigrade. The abrupt delivery of cold, denser, creek water into warm, less dense, lake water produced a situation in which the tracing of the spread of the stream in the lake was a simple matter. Water from the stream did not mix readily with that of the lake, but had a distinct tendency to flow under it and spread along the bottom. The creek water maintained its integrity for some distance. It was quite distinguishable from lake water by its lower temperature. On August 5, 1940, presence of creek water 150 meters lakeward from the mouth of the stream was evidenced by a temperature

of 18.9° Centigrade on the bottom, while the temperature of the lake water at the surface was 22.5° Centigrade. The depth at that point was about 1 meter. Contrasting conditions at a point approximately 400 meters farther east and 250 meters from shore showed homothermous water with a temperature of 23.5° Centigrade at a point where the depth was slightly more than 1 meter. The spread of creek water in the region of the lake immediately around the mouth of the stream was studied by comparing the temperature of surface water with that of bottom water. On July 30, 1940, two transects, along which top and bottom temperatures were measured, extended from approximately the middle of the creek current, at right angles to the main flow, westward to a point where warm homothermous lake water was reached (Fig. 6). On August 3, similar transects were established eastward. The temperature records on the map indicate spread of creek water and lack of mixing of creek and lake water. The direction of the wind altered the direction of the creek current in the lake. On August 5 additional temperature transects were made radiating from a point in the lake about 60 meters from the mouth of the creek. These radii were 90 meters long and extended west, southwest, south, southeast, and east. The depth was less than 1 meter.

In comparison of the distribution of creek animals (Fig. 5) with the spread of creek water (Fig. 6) it is seen that the creek animals were not restricted to the area covered by the creek water, nor did they follow the course of the creek water in the lake; but rather were restricted to the region quite near the mouth of the creek and spread somewhat along shore in both directions.

#### WATER LEVEL AND DRIFT

During the summers of 1940 and 1941 the fall of surface level of Burt Lake caused marked changes in the stream bed for a distance of at least 85 meters upstream from the mouth. In early summer the stream bottom in this portion of the creek was eroded only slightly, and consequently there was only a minimal deposition of creek sand to form the terminal delta just within the mouth of the creek (Fig. 7). As the surface level of Burt Lake fell, the slope between creek level and lake level became steeper, producing swifter current and greater bottom erosion. In early summer the stream bottom, from the region of the mouth to at least 85 meters upstream, was richly populated with animals. The particulate debris and stand tubes of chironomid larvae made a dark brown mat over the grayish yellow sand beneath. When erosion increased this mat was broken up and much of the substratum of sand drifted lakeward to the delta. On entering Burt Lake, Carp Creek began to drop its load. Sand settled on the lakeward extremity of the delta and the drift animals sank to the bottom only a few meters farther lakeward, forming concentration zones. Position and shape of the newly forming delta changed daily. The delta



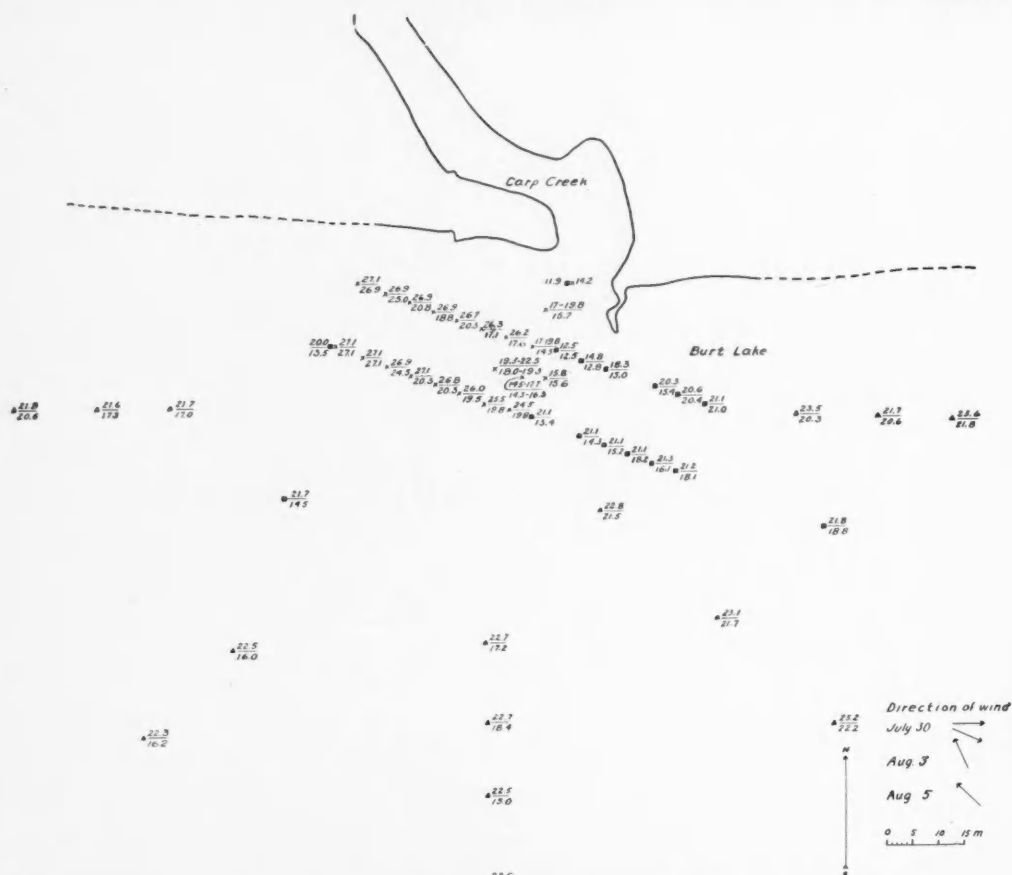


FIG. 6. Map showing water temperatures in Burt Lake near Carp Creek. Station symbols for different dates are as follows: cross, for July 30; square, for August 3; and triangle for August 5. All dates were in 1940. Numbers indicate temperature in degrees Centigrade. Surface temperature above and bottom temperature below the line. Arrows indicate wind direction on different dates.

grew beyond the mouth of the creek and extended several meters out over the lake bottom. Heavy wave action obliterated this delta, forming beaches and islands out of its materials, but during periods of calm the constant erosion of creek bottom led to the rebuilding of other deltas, frequently more than one (Figs. 7-14). As new deltas were formed new zones of concentration of drift animals developed in the regions immediately lakeward from them.

#### BURIAL IN THE DELTA

While the delta was changing position and extending farther out over the lake bottom, drift animals were settling on areas soon to be covered by the delta. The delta was studied to determine whether any considerable quantity of drift animals was buried by it.

On July 2, 1941, there was a prominent delta at the mouth of Carp Creek, because the weather had been calm for a day or two. The delta was approximately 20 centimeters thick at a point 2 meters upstream from its lakeward margin.

In order to obtain information for answering the question concerning burial or drift animals, the inverting bottom sampler was used as a core sampler.

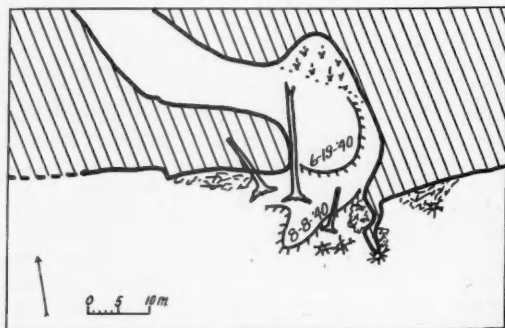


FIG. 7. Map of mouth of Carp Creek and immediate vicinity showing positions of the delta June 19 and August 8, 1940. Fringed line represents lakeward limit of delta.

Samples were taken to determine whether buried drift animals, or parts of animals, could be recovered from the delta material. Previous samples in the upper layers of the delta showed few animals in

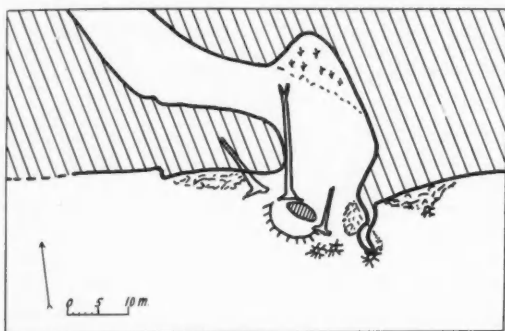


FIG. 8. Map of mouth of Carp Creek and immediate vicinity showing position of delta and an island formed of delta material, August 15, 1940. Fine hatching represents delta material above water level.

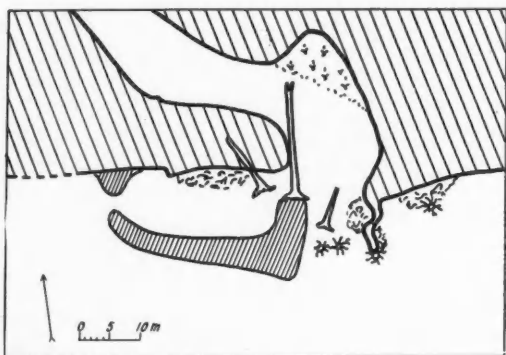


FIG. 9. Map of mouth of Carp Creek and immediate vicinity showing position of an island formed from delta material, July 21, 1941.

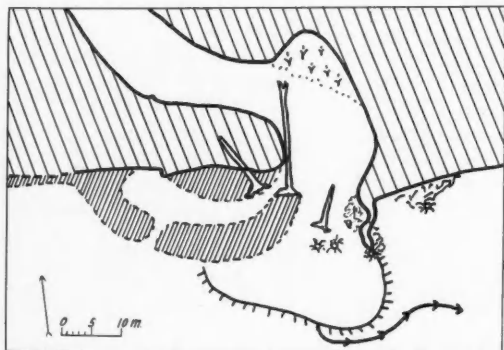


FIG. 10. Map of mouth of Carp Creek and immediate vicinity showing general position of the delta and an arrowed line indicating the course taken by a larva of *Brachycentrus americanus* during 5 hours on August 1, 1941. Dotted lines show approximate position of island and beach formed of delta material.

that part. Trial samples were collected to determine the depth from which it would be necessary to obtain a sample containing debris similar to that material lakeward from the delta. This material appeared to be the debris which, a few days before, was lakeward from the delta then existent. It was about 20 centimeters below the surface of the delta.

The top layer of the delta material, about 15 centimeters thick, was removed from an area of approximately 0.5 square meter. No debris was uncovered during this removal. From the middle of the depression resulting from removal of delta material

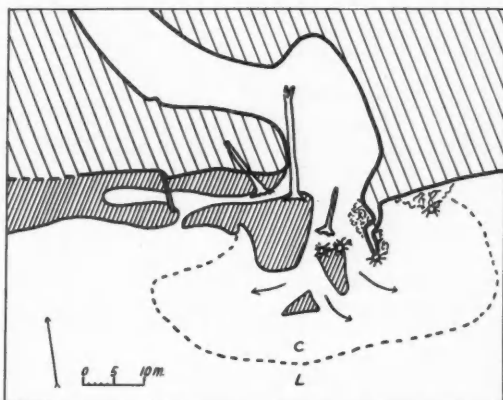


FIG. 11. Map of mouth of Carp Creek and immediate vicinity showing direction of spread of creek during a storm from the south at 5 p.m. on August 11, 1941. The dotted line shows approximately how far the turbid lake water (L) extended over the outflowing creek water (C).

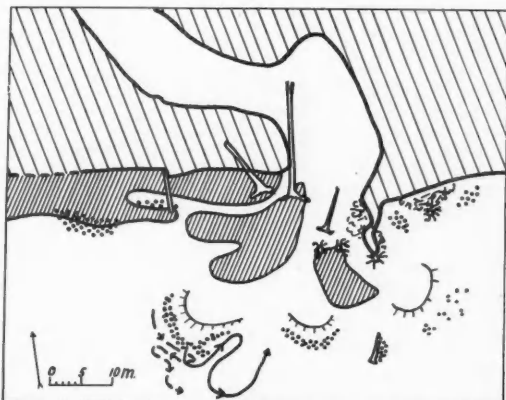


FIG. 12. Map of mouth of Carp Creek and immediate vicinity showing positions of animals and debris along the beach, in concentrations resulting from wave action on August 11, and of zones of concentration built up lakeward from the delta during about 24 hours of calm, August 12, 1941. Dots represent concentrations of debris and animals. Observed movements of two animals around edge of delta, during about 15 minutes each, are indicated. The broken arrow line shows course followed by individual of *Sparganophilus* sp., and the continuous line shows that followed by an individual of *Gammarus limnaeus*.

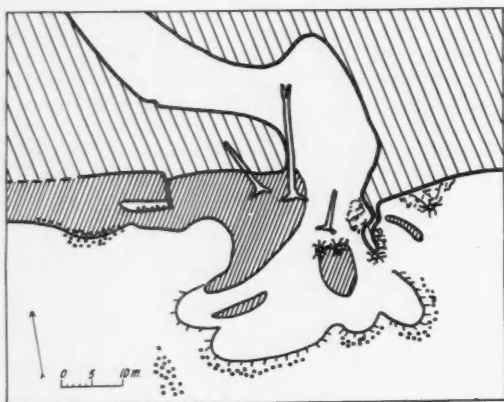


FIG. 13. Map of mouth of Carp Creek and immediate vicinity showing position of delta and debris after several days of calm, August 21, 1941.

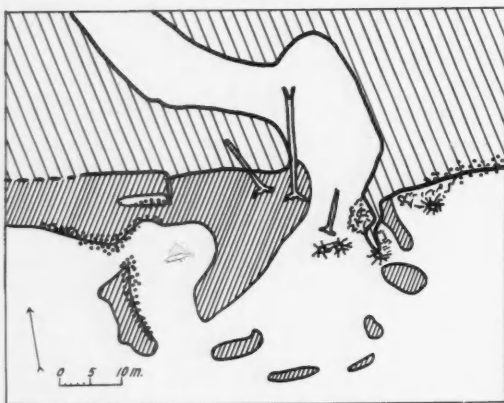


FIG. 14. Map of mouth of Carp Creek and immediate vicinity after south winds and considerable wave action, 8 p.m., August 23, 1941, showing islands composed of delta material piled up by waves; also concentrations of animals and debris on the beach.

several bottom samples were collected. The cylindrical samples were composed of yellowish sand on top and darker lake material on the bottom, separated by a layer or two of black debris. This debris, the layer of delta material about 1 centimeter thick immediately above, and about 1 centimeter of lake bottom were the only portions saved. These samples were taken to the laboratory, where they were examined with a binocular dissecting microscope. Some almost complete chironomid exuviae and many apparently exuvial parts were found. Carcasses, either fragmentary or entire, which would indicate burial of living or recently dead animals were not discovered. If burial was of much importance in the fate of drift animals it seems that at least some of the buried animals would have been discovered. That such animals were overlooked in the samples is unlikely, for exuviae and heavily sclerotized parts of the insects were easily and frequently observed, al-

though these parts were much harder to detect than an entire animal would have been.

Although this sampling was inadequate to permit an accurate estimate of how much burial of drift animals occurs, it does indicate that the number of animals suffering this fate is comparatively small.

#### EFFECT OF BOTTOM EROSION ON CREEK POPULATION

During the interval between June 16 and July 19, 1941, the surface level of Burt Lake fell about 17 centimeters. During this period, erosion formed a new submerged channel occupying about the middle third of the stream bed for a distance upstream from the mouth. During the two previous summers the erosion was less severe. On July 1, 1940, the stream bottom about 25 meters from the mouth of the creek was not eroded. Particulate debris and sand tubes of chironomid larvae formed a dark brown mat over the yellowish sand. Three bottom samples were collected in this area, data from which are shown in Table 5 under columns A, B, and C of transect I. Samples A and C were collected about 1 meter from the south and from the north margins of the stream respectively. Sample B was from the middle of the stream. Using data from these samples as a basis for computation, the average number of animals in the area sampled was more than 944.8 per 100 square centimeters. Data in columns A, B, and C under transect II are from samples collected July 25, 1940, at approximately the same places as those on July 1. No submerged channel was present at this transect, but erosion had removed much of the mat from the creek bottom. Data from these samples indicate an essential uniformity across the transect. The average population for the transect on this date, using these data for computations, was only about 55.5 animals per 100 square centimeters. The reduction in size of population showed that a large number of creek animals had disappeared from the area. On August 9, 1940, an erosion channel about 3.5 meters wide and 0.25 meter deep was in the middle of the creek 25 meters upstream from the mouth. Data in columns B and C, compared with those of A and D under transect III, show marked reduction of animals in the erosion channel of the stream. The population computed for the erosion area was approximately 13.7 animals per 100 square centimeters. The uneroded margins averaged 345.4 animals per 100 square centimeters. Sample A was from the south margin of the creek and sample D from the north. The latter sample was from an area where very dark particulate debris covered the sand, and a bed of *Ranunculus longirostris* Gordon protected the bottom from current. The presence of a large number of animals in the sample from this protected area indicated that erosion of the bottom, rather than seasonal or life history changes caused the reduction in size of population in the middle of the stream.

In 1941 the fall of surface level of Burt Lake came much earlier than in 1940. In June 1941, the erosion

TABLE 5. Effect of bottom erosion on creek population. Dates of transects: I, July 1, 1940; II, July 25, 1940; III, August 9, 1940; and IV, June 18, 1941. Letters A, B, C, and D refer to individual samples. Numbers refer to animals per 100 square centimeters. Asterisks indicate samples from erosion channel.

	Transects in creek bottom before erosion of channel						Transects in creek bottom after erosion of channel							
	I			II			III				IV			
	A	B	C	A	B	C	A	B*	C*	D	A	B	C*	D
Oligochaeta.....	38.5	29.4	11.3	2.3	.....	2.3	.....	.....	.....	2.3	.....	2.1	.....	2.1
Sphaeriidae.....	2.3	.....	.....	.....	.....	.....	.....	.....	.....	2.3	2.1	2.1	2.1	10.5
Asellus communis.....	2.3	2.3	6.8	.....	.....	.....	.....	.....	.....	.....	25.3	.....	.....	.....
Gammarus limnaeus.....	2.3	4.5	.....	.....	6.8	.....	.....	.....	.....	6.8	8.4	8.4	2.1	6.3
Baetis brunneicolor.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	2.1
Pentaneura sp.....	2.3	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Procladius sp.....	6.8	.....	.....	.....	.....	.....	.....	.....	.....	2.3	4.2	.....	.....	2.1
Procladius sp.....	24.9	13.5	18.1	11.3	.....	4.5	.....	2.3	2.3	9.1	8.4	29.5	6.3	12.6
Diamesinae.....	2.3	2.3	6.8	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Orthocladinae.....	9.1	.....	2.3	.....	.....	.....	27.2	.....	.....	18.1	46.3	33.7	.....	52.6
Corynoneura sp.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	2.3	.....	.....	.....	.....
Trichocladus n. sp.....	45.3	27.2	6.8	.....	.....	.....	11.3	.....	2.3	13.6	46.3	80.0	.....	242.1
Chironomus (Harnischia ?) sp.....	24.9	4.5	2.3	4.5	.....	.....	2.3	.....	15.8	2.3	23.2	23.2	.....	2.1
Orthocladinae.....	4.5	9.1	.....	.....	.....	.....	4.5	.....	.....	6.8	.....	.....	.....	.....
Tanytarsus confusus (?).....	375.7	620.2	848.9	9.1	6.8	.....	29.4	.....	.....	416.5	113.7	421.1	.....	806.3
Tanytarsus sp.....	.....	.....	.....	.....	.....	.....	.....	.....	2.3	.....	.....	.....	.....	.....
Endochironomus sp.....	291.9	215.0	149.4	43.0	56.6	11.3	31.7	2.3	.....	95.1	130.5	73.7	.....	235.8
Cryptochironomus sp.....	.....	4.5	6.8	2.3	.....	2.3	2.3	.....	.....	.....	2.1	.....	.....	.....
Chironomus (?) spp.....	2.3	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Chironomid pupae.....	2.3	4.5	.....	.....	.....	.....	4.5	.....	.....	.....	2.1	16.8	.....	33.7
Rhagionidae.....	.....	.....	.....	4.5	.....	.....	.....	.....	.....	.....	.....	2.1	.....	.....
Ceratopogonidae.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	6.3	2.1	.....	.....
Total.....	837.7	937.0	1059.5	77.0	70.2	20.4	113.2	4.6	22.7	577.5	418.9	694.8	10.5	1408.3

channel was well developed. Transect IV was made 85 meters upstream from the mouth of the creek, where the erosion channel in the bottom was about 3 meters wide and 0.5 meter deep. A wide expanse of uneroded bottom covered by shallow water extended along the margins of the stream. Samples A and B were from the uneroded area on the south side of the creek; sample C from the erosion channel; and sample D from the uneroded margin on the north. Using data from samples A, B, and D, the average population for the uneroded area was 840.7 animals per 100 square centimeters, while that for the channel was only 10.5.

These data are too meager to allow more than a rough estimate of the size of the population, yet it is thought that a fairly representative picture is given here. Scattered samples, not collected along transects, and hence not included in these tables, serve as the basis for this opinion.

These data show that: (1) uneroded bottom of Carp Creek supported a large population of animals; (2) general erosion of creek bottom reduced the number of animals in certain areas; and (3) erosion of a channel in the creek bottom reduced the size of the population very markedly in the eroded area.

The surface level of Burt Lake bore an important relation to the erosion in Carp Creek, at least within 85 meters upstream from the mouth. The presence or absence of erosion determined whether or not bottom animals were washed away from their positions. Many bottom animals which were washed away as the

water eroded the bottom would not have become drift animals if the lake level had remained unchanged. To this extent the lowering of the surface level of Burt Lake influenced the quantity and quality of animals carried into it in stream drift.

The position and formation of the delta determined to some extent where the creek dropped its load and hence had some influence on at least the temporary fate of the drift organisms. As the surface level of Burt Lake fell the delta progressed farther lakeward and concentrations of creek animals developed farther out on the lake bottom.

## LAKE INFLUENCES

### WAVE ACTION

*Intensity.* Animals drifting out of Carp Creek arrived in a portion of Burt Lake protected from the prevailing northwest winds. The occasional winds and storms from the south and southeast had a sweep of about 9.5 miles, and produced considerable wave action on the gradually sloping shoal south of the mouth of the creek. When whitecapped waves were produced by southerly winds a heavy surf pounded the beach at the mouth of Carp Creek. Under such conditions rooted vegetation, lake animals, and stream animals were washed upon the beach.

*Effect on Creek Animals in Concentration Zone.* During the first week in August, 1941, there was slight to moderate wave action in Burt Lake near the mouth of Carp Creek. On August 8, blackish

debris, typical of the zone of concentration, was present on the lake bottom near the delta. During the next few days winds were shifting. On the morning of August 11, there was a strong wind from the southeast. The direction of the wind shifted to south, then to southwest by late afternoon. On August 12, the wind was from the northwest. During the southerly winds on the former date the area around the mouth of Carp Creek was subjected to vigorous wave action. By late afternoon of August 11, the waves had altered the position of delta material to such an extent that the area of flowing creek water divided off into 3 currents, two moving eastward and one westward (Fig. 11). The edge of the delta was poorly defined and no debris remained on the bottom in this area except at a point about one meter southeast of the island which separated the west part from the middle part of the current. Before wave action ceased, on August 11, three series of bottom samples were obtained: 5 samples from positions where the zones of concentration existed prior to the storm; 2 samples from the area between the west and middle portion of the stream; and one sample from a location about 5 meters farther lakeward in an area protected from vigorous wave action by a log on the bottom. After about 24 hours of calm weather conspicuous masses of debris on the lake bottom marked the zones of concentration of creek animals near the delta and along shore east and west of the creek (Fig. 12). Three bottom samples were collected August 12, from the zone of concentration lakeward from the delta. On August 15, a very heavy accumulation of debris was present a few meters lakeward from the delta produced by the western part of the current. Other more scattered masses of debris were located lakeward from

the deltas produced by the middle and eastern portion of the current. Three samples were collected from these zones of concentration. Data from samples taken during both wave action and calm (Table 6) show that several hours of wave action distinctly reduced the number of creek animals in zones of concentration, but that a day of calm allowed drift materials and animals to collect in conspicuous quantities in areas lakeward from the newly formed deltas. These areas were the beginnings of new zones of concentration.

Protection from wave action seemed to enable the creek animals to maintain their positions in the lake. In one location the eddies between the middle portion of the creek current and the water immediately to the west evidently set up some sort of protection for the animals and debris on the bottom, while in another area protection was supplied by a log on the lake bottom. These facts show that many of the animals in the zone of concentration lakeward from the delta of Carp Creek were unable to maintain their positions when exposed to vigorous wave action.

*Effect on Bottom.* During high water, before the delta extended out into the lake, the zone of concentration of creek animals around the edge of the delta was somewhat protected by the stumps at the mouth of the creek. Later, when the water was shallower, the delta projected lakeward and the region where the creek animals collected in calm weather received vigorous wave action during storms. A few hours of wave action caused by southerly wind following a period of calm made striking changes in the shape of the delta, its position, and even the direction of flow of creek water. Delta materials were formed into islands, spits, and beaches by waves from one direction, but were shifted to new positions by waves

TABLE 6. Effect of wave action on animals in zone of concentration. Each column represents 1 bottom sample, numbers indicate animals per 100 square centimeters. A. August 11, 1941; exposed to direct wave action; B. August 11, 1941; protected between deltas; C. August 11, 1941; protected by log on bottom; D. August 12, 1941; calm; E. August 15, 1941; calm.

	A					B		C	D			E		
CREEK ANIMALS:														
Sphaeriidae.....							2.1			2.1	4.2			4.2
Asellus communis.....	2.1						4.2							
Gammarus limnaeus.....									18.9	6.3	2.1	6.3		12.6
Tanypodinae.....												2.1		
Prodiamesa sp.....						10.5	4.2	4.2	2.1	4.2	23.2	10.5	2.1	2.1
Trichocladius n. sp.....					2.1	4.2	4.2	2.1						
Orthocladinae.....	6.3					2.1	12.6	6.3	10.5	8.4	4.2	2.1	6.3	2.1
Tanytarsus confusus (?).....								2.1				2.1	4.2	
Chironomus (Harnischia ?) sp.....			2.1				8.4			2.1				
Endochironomus sp.....						12.6	4.2	8.4	4.2		6.3	2.1		12.6
Cryptochironomus sp.....	4.2	2.1					2.1		2.1	10.5	4.2			
LAKE ANIMALS:														
Oligochaeta.....	27.4	58.9	2.1	14.7	6.3	16.8	6.3	29.5	8.4	18.4	42.1	67.4	6.3	6.3
Hirudinea.....								2.1			2.1			
Gastropoda.....											2.1			
Hyalella azteca.....								4.2						
Tanytarsus sp.....	2.1	6.3						42.1			2.1			
Polypedilum flavus (?).....	2.1	4.2	2.1			8.4		6.3	6.3			2.1		
Cryptochironomus n. sp.....		2.1				2.1			2.1					
Pseudochironomus sp.....	10.5	10.5	4.2	10.5	2.1		2.1		8.4	8.4		2.1	10.5	4.2
Ceratopogonidae.....	2.1	6.3						2.1			8.4		6.3	



from another direction. A series of maps, with beaches, islands, and deltas indicated, gives an idea of the changes observed (Figs. 7-14).

**Effect on Drifting Animals.** In order that the effects of waves on drifting creek animals might be studied, glass-bottomed buckets were employed so that direct observations might be made. This method was used in all types of weather, from calm to a heavy storm. Because it was impracticable to observe all types of drift animals, since some of them were minute and inconspicuously colored, this portion of the work was restricted to the more abundant and larger kinds. The animals observed were the following: Chironomidae, *Gammarus limnaeus*, *Asellus communis*, Trichoptera, and *Sparganophilus* sp. (the only oligochaete sufficiently conspicuous to be followed by this method). Many typical drift animals were observed as they were washed into the lake and as they settled to the bottom near the edge of the delta in calm weather, or as they struggled against waves during storms. Each kind of animal manifested certain characteristic activities. Further data were obtained by experiments. Living animals were collected from the creek and released near the edge of the delta to drift into the area visible under the glass-bottomed bucket. Activities of transplanted animals were typical of the groups to which these animals belonged. Activities which seemed significant in determining the fates of these animals were as follows:

*Gammarus limnaeus*: These animals practically always attempted to burrow in the sand or debris just lakeward from the delta. In calm weather burrowing took only a few seconds. Wave action usually disturbed the burrowing process and caused the animals to swim in circles. Waves sometimes dislodged individuals which had been able to burrow. Continued disturbance and active swimming evidently exhausted these animals, for they soon became passive and were washed about by the waves as if dead. Sometimes these animals clung to bits of debris and were rolled about from place to place during wave action. Occasionally an individual became attached to a bubble and floated upward into the waves or into the creek current before the bubble burst at the surface, allowing the animal to settle several meters away.

Chironomidae, mostly *Procladius* sp. and *Trichocladius* sp., also a few *Endochironomus* sp. and *Tanytarsus confusus* (?): Usually chironomids were able to burrow, but less rapidly than gammarids. Most of the individuals were able to burrow completely out of sight within about 30 seconds after arriving at the bottom. Wave action disturbed burrowing activities and caused the animals to wriggle violently. These wriggling movements frequently raised the animals off the bottom into currents of water. When wriggling ceased the animals settled into other positions, the locations of which were dependent on the direction of the current.

*Asellus communis*: These animals settled to the bottom and crawled on the sand; evidently in

search of debris, for they remained active until they crept under something. During wave action they were rolled about with the objects to which they were clinging.

Trichoptera, mostly of Limnophilidae and *Brachycentrus americanus*: None of these animals seemed to be content to remain in concentration zones, but restlessly attempted to crawl elsewhere. Usually the motion was in the same direction as that of the currents. When disturbed by wave action these animals usually retracted into their cases and were rolled about. Individuals of *Brachycentrus americanus* frequently crawled up on leaves of *Potamogeton* sp. and hung by threads. Usually the threads broke very soon and the animals were washed a few centimeters farther as they fell.

*Sparganophilus* sp. (only three were observed): Only moderate wave action was sufficient to prevent these animals from burrowing. They washed about helplessly in creek and lake currents.

During very rough weather it was impracticable to follow an animal for more than a few minutes because of the waves and the high turbidity in the lake water during such conditions. During one storm from the south when the lake water was particularly turbid the creek water remained quite clear, and only in the region of the mouth of the stream where creek water was not covered by lake water was the bottom visible. The extent of the creek water not covered with turbid lake water is shown in Figure 11. This roughly corresponded to the lakeward limit of the delta.

In times of calm or of moderate wave action it was possible to follow actions of individual animals with comparative ease.

The addition of drift animals to zones of concentration around the lakeward margin of the delta was observed in calm weather. Onshore waves washed these animals from their new positions and carried them shoreward.

As trichopterous larvae did not remain in the zone of concentration even during calm weather, one individual of *Brachycentrus americanus* was followed for 5 hours. Figure 10 shows the route taken by this animal during the period of observation. Other individuals which were seen with the one being followed all displayed essentially the same activities. Behavior of these animals is included in the foregoing records.

During the period of several days preceding August 7, 1941, the wind was from the north or northwest and caused little wave action at the mouth of Carp Creek. A considerable amount of drift material had settled on the bottom around the lakeward edge of the delta. During early morning on this date there was a breeze from the southwest only, but by late forenoon a brisk wind developed from the same direction, causing an alongshore current moving eastward in the region of the mouth of the creek. On the bottom, in areas where the creek water formed a

layer below the warm lake water, this alongshore current was hardly noticeable and did not affect the debris or animals in the concentration zones, except when waves churned the water to such an extent that bottom materials were lifted into the alongshore current. When this happened the animals were transplanted a few centimeters eastward by the alongshore current and a short distance shoreward by the wave action before they settled to new positions on the lake bottom. If the creek current hit the animals they were washed farther lakeward. The combination of creek current, alongshore current, and wave action carried animals eastward along the lakeward edge of the delta, then shoreward. By the middle of the afternoon there was a scattered mass of debris and stream animals up on the beach approximately 25 meters east of the creek, a region from which such material had been absent a few hours earlier. In the shallow water along this beach a large concentration of material, similar to that around the lakeward margin of the delta, was present. Some of this material was washed ashore by almost every large wave. In the material on shore the following Carp Creek animals were seen: 12 of *Gammarus limnaeus*, 1 of *Asellus communis*. Animals which may have been from either creek or lake were: 1 of *Sparganophilus*, only a fragment, 1 chironomid pupa, 2 larvae of *Orthocladinae*, 1 of *Tanypodinae*, and 1 of *Hydropsychidae*. The area observed was only a meter or less wide and about 3 meters long. No attempt was made to take a complete census of the animals in the debris, but only a check to determine whether creek animals had been washed ashore in the region where none were present a few hours before. On the following day individuals of *Gammarus limnaeus* were abundant on the portion of the beach described. Chironomid larvae, probably *Trichocladus* n. sp. and *Procladius* sp., the species usually seen, were fairly abundant.

These observations showed that Carp Creek animals can be washed up on the beach east of the creek within a few hours by waves resulting from a southwest wind.

**Results.** During calm weather or in periods of slight wave action creek animals and debris collected in a zone of concentration around the lakeward margin of the delta (Figs. 12, 13). During more vigorous wave action the accumulation of animals and debris shifted to new positions, usually east and west of the creek (Fig. 14). Secondary zones of concentration were thus established in the shallow water near the beach. The latter zones were frequently about 1 meter wide at the widest point and up to about 10 meters long. A mass of roots along the shore or a log on the bottom often seemed to be the center about which the debris and animals collected. The force and direction of wind, alongshore current, and waves influenced the position of these concentrations along the shore.

During one of the heavy storms a mass of debris and creek animals occurred at the water's edge about

25 meters west of the creek. Waves gradually washed this material up on the beach. This mass teemed with individuals of *Gammarus limnaeus*, and chironomid larvae, mostly *Procladius* sp. and *Trichocladus* n. sp.

There were at least two important results of wave action: (1) the shifting materials of the delta were carried shoreward, and formed into spits, islands, and beaches; and (2) the major portion of the debris and animals in the zone of concentration just lakeward from the delta were washed upon the nearby beach.

The question arose whether or not these stream animals could maintain themselves in the lake environment. In search of the answer, several experiments were made. Typical creek animals commonly found in drift samples and bottom samples near the mouth of the stream were transplanted to several stations in the lake to determine whether they would remain there.

#### TRANSPLANTATION EXPERIMENTS

Evidence given previously (Fig. 5) indicates that drift animals settle on the lake bottom near the mouth of the creek. In order to learn something about the factors that limit the distribution of stream animals to this restricted area of the lake some transplantation experiments were conducted. In these typical stream animals were transplanted to lake bottom in locations beyond the influence of the creek, but much like the area where drift animals settled.

**Experiment I.** The purpose of this experiment was to determine whether creek animals, when placed on the lake bottom in warm lake water, would become sufficiently established in the new environment to maintain their positions in the area. Similarities between the station selected for this experiment (Fig. 1, a) and the region lakeward from the mouth of the creek where much drift material settles were: (1) distance from shore about 25 meters; (2) presence of sandy shoal exposed to the waves produced by winds from the south; and (3) depth of water about 0.7 meter. The chief points of difference were that the station for this experiment was: (1) about 400 meters east of rather than directly lakeward from the creek mouth; and (2) in warm lake water instead of cold creek water. The selection of the exact spot for this station was made at random. The area, about 0.4 square meter, used in this experiment was marked by four stakes. Animals for the transplant were obtained from the bottom of the creek. About four liters of bottom material, which included approximately 15,000 animals, were collected and placed in a bucket. In order to avoid suffocation of the animals in the bucket they were carried to the selected area immediately and transplanted. Bottom debris was transplanted with the animals in preference to sorting out the animals and subjecting them to possible injury.

The transplantation was accomplished by lowering the bucket to the lake bottom and inverting it so that the contents would fall out. The bucket was held

upside down a few centimeters above the sand until the animals and debris had settled to the lake bottom, and then was lifted slowly, in order to avoid disturbance of the transplanted material. The creek material was spread over the chosen area as uniformly as was practicable. An approximate measure of the density of the population in this newly transplanted material was secured by obtaining a bottom sample, taken with the inverting sampler, immediately. In order to discover any change in this population additional bottom samples were collected after (1) three hours, (2) two days, and (3) two weeks. In order to determine what lake animals might be expected in the samples from the experiment, bottom samples were collected from the transplantation area shortly before the addition of creek materials, and from the lake bottom about 3 meters farther west two days after the beginning of the experiment. This experiment began in late forenoon June 18, 1941, during calm weather which lasted until the middle of the morning June 20. Examination of the bottom samples showed no decrease in population during the first three hours. Creek animals lived on the lake bottom for two days in calm weather, and at least a portion of them remained in the area where they had been placed. The sample collected the second day contained fewer experimental animals than samples obtained the first day. From information in other experiments it now seems probable that the reduction in population was due to scattering of the transplanted animals or loss by predatory activities of fishes, rather than to chemical or temperature differences encountered in the new environment. The animals of significance in this experiment, since they were characteristic of Carp Creek but not of Burt Lake, were *Prodiamesa* sp., *Tanytarsus confusus* (?), and *Trichocladus* n. sp. The last-named species was represented by one individual in the bottom sample collected in the transplant area before the addition of creek animals, but no other specimen of this kind was collected in lake water away from creek influence during the entire investigation. Hence that individual was considered as a rare exception. Representatives of *Endochironomus* sp. occurred in both creek and lake, but usually were much more abundant in the former. The absence of this species from the sample collected two weeks after the transplanting suggests that even these animals could not withstand wave action, for a period of rough weather occurred during the two weeks they had been on the lake bottom. This experiment showed that some creek animals in warm lake water lived and maintained their positions on lake bottom for at least two days. The absence of creek animals after a period of wave action indicated that wave action possibly caused their disappearance. However, too much time elapsed between the collecting of the sample during calm weather and the sample after the storm for it to be certain that other factors were not involved.

Experiment II. The purpose of this experiment was to determine whether strong wave action would prevent establishment of creek animals on the bottom

in an area near the shore. The station chosen for this experiment (b in Figs. 1, 2) was about 25 meters west of the mouth of Carp Creek, 2 meters from shore, and in water about 0.3 meter deep. In late forenoon, June 20, 1941, there was a brisk southwest wind causing vigorous wave action along the beach west of Carp Creek. The station for this experiment was marked with stakes and a bottom sample was collected from the area. Creek animals were collected in essentially the same manner and quantity as in Experiment I and were transplanted in the same way. In the presence of considerable wave action the creek material did not settle readily to the bottom, but was scattered by the waves. A bottom sample was collected from the transplant to determine approximately the abundance of the animals at the beginning of the experiment. In a few minutes the transplanted material became widely scattered. Bits of debris, and some pieces of *Ranunculus* sp. which were included in the transplant, were washed along the beach and into a mass of roots nearer the mouth of the creek. At the end of an hour no visible trace of the black bottom material was left in the area marked off by the stakes. A bottom sample collected from that area contained no animals. The sample collected before addition of creek material contained only one small larva of *Orthocladinae*. The sample obtained in the transplantation area before the transplant was washed away included 32 animals. It is certain that waves in combination with alongshore current washed these animals from the transplantation area.

The final fate of the animals in this experiment is unknown. Because of the presence of masses of roots and drift wood along the beach immediately west of the mouth of the creek, it could not be determined whether the animals were washed ashore. The fact that some of the bits of *Ranunculus* sp. became tangled in the roots was an indication that animals met the same fate. Possibly these experimental animals did not remain in the area because, owing to the wave action, they did not have sufficient time to burrow in the sand. Similar inability of drift animals to become established around the mouth of the creek during storms will be discussed later.

Experiments I and II were not comparable because neither weather conditions nor the distances from shore were the same in the two experiments. For the sake of brevity the data from these two experiments have been omitted from Table 7. Two other experiments (III and IV) were conducted at different distances from shore, but concurrently in order that they should be comparable.

Experiments III and IV. The purpose of these experiments was to determine (1) whether transplanted creek animals could maintain their positions more successfully in water 4 meters from shore, or about 30 meters farther lakeward, and (2) whether stream animals transplanted west of the creek would respond differently from those transplanted about the same distance from the shore east of the creek. Stations chosen for these experiments were about 420

TABLE 7. Data from transplantation experiments. Columns under Experiments III and IV represent bottom samples; those under V and VI represent only the portions of the transplants examined.

Animal	Experiment III					Experiment IV					Experiment V		Experiment VI	
	Burt Lake before transplantation	Transplant area after 1 hour	Transplant area after 5 hours	Transplant area after 1 day	Transplant area after 3 days	Burt Lake before transplantation	Transplant area after 1 hour	Transplant area after 5 hours	Transplant area after 1 day	Transplant area after 3 days	Dead animals	Living animals	Dead animals	Living animals
<i>Oligochaeta</i> .....		11	3	5	3			4	1	3		3		12
<i>Hirudinea</i> .....			1					1			1	2		1
<i>Sphaeriidae</i> .....		16	2	5	6		5	2	5	8		3		
<i>Asellus communis</i> .....		2					2							4
<i>Gammarus limnaeus</i> .....		48	9	16			18	5			7	5		7
<i>Tipulidae</i> .....							1					1		
<i>Tanypodinae</i> .....		4	1				1	1				4		2
<i>Prodiamesa</i> sp.....		33	3	27	1		17	1	5	11		26	2	19
<i>Orthocladinae</i> .....		4	7	1			10		3					1
<i>Trichocladus</i> n. sp.....		38	8	4			22	3	1	1		4		
<i>Chironomus (Harnischia ?)</i> sp.....		2		1			4		1			1		
<i>Tanytarsus confusus</i> (?).....		157	28	30			97	11	15	29	17	314	12	33
<i>Colypedilum flavus</i> (?).....			1		1		1	4	3	6				1
<i>Pndochironomus</i> sp.....		72		43	33		14	7	18	72		33		18
<i>Eryptochironomus</i> sp.....		2	1				2							
<i>Cryptochironomus</i> n. sp.....		1	4						1	1				
<i>Chironomus</i> (?) spp.....					1									
<i>Chironomid pupa</i> .....		6	1	1			1							
<i>Pseudochironomus</i> spp.....		3	5	5	3									
<i>Rhagionidae</i> .....							1					5		
<i>Ceratopogonidae</i> .....														1
<i>Hydracarina</i> .....		2							1	6		1		
Total.....	4	406	70	136	51	4	196	39	54	137	25	406	14	99

meters west of the mouth of the creek (Fig. 1, e), definitely out of the influence of stream water. The areas were on a sandy shoal very similar to the location chosen for Experiment I. The exposure was a little more westerly and the water slightly shallower, but other features were essentially alike. The station for Experiment III, 4 meters from shore, was in water about 0.3 meter deep. This location was chosen because (1) it was at the shoreward margin of the very gradual slope of the lake bottom and was just lakeward from the steeper slope near the shore, yet (2) was near enough to shore to be affected by the bottom currents resulting from the wave action in times of south or southwest winds. Experiment IV, about 34 meters from shore, was in water approximately 0.5 meter deep. This location was chosen because it was (1) about the same distance from shore as Experiment I, (2) about as far from shore as the lakeward limit of the area where much stream drift material settled on the lake bottom, and (3) in only slightly deeper water than Experiment III. Bottom samples for lake animals were collected from both stations and stakes were driven to mark the areas.

Approximately the same quantity of stream animals and bottom materials as used in Experiment I was screened, then concentrated in a cloth net to a volume of about 2 liters and quickly carried to each area for transplanting. The animals apparently suf-

fered no ill effects from this treatment. The net was more efficient than the bucket used in Experiment I and II, for when using the former the transplant material could be placed directly on the desired area. Transplantation was accomplished by constricting the net above the contents with one hand, placing the rim of the net on the bottom of the lake with the other hand, finally everting the net and leaving the transplant on the designated spot. Transplant material was obtained in creek water at a temperature of 13.5° Centigrade and placed in lake water at 22° Centigrade.

A few minutes after creek material was placed on the lake bottom in Experiment III a school of about 24 small fishes (sp. ?) began to feed in the transplant. No fishes were seen during Experiment IV.

In order to discover any decrease in the number of animals in the transplants during Experiments III and IV, bottom samples were collected from these areas after intervals of 1 hour, 5 hours, 1 day, and 3 days. Mild wave action during comparatively calm weather throughout these 3 days resulted in almost total elimination of creek animals from the area used in Experiment III (Table 7). However, in the area used in Experiment IV the transplanted animals remained fairly abundant, except that *Gammarus limnaeus* was not represented in the last two samples collected from that station. It is possible



that the disappearance of gammarids from these areas was partly due to their habit of swimming actively rather than hiding when disturbed. This behavior would scatter the population rapidly and make the individuals more subject to predation than other animals in the transplant.

Results from Experiments III and IV indicated that creek animals were able to live in lake water, but were not able to withstand the action of waves, and perhaps predation by minnows.

Experiment V. The purpose of this experiment was to determine whether there was anything concerning the chemistry and temperature of Burt Lake water or anything present on the bottom which would prevent Carp Creek animals from living in the lake if they were protected from the mechanical action of waves and from predation by fish. The position chosen for this experiment was only a few meters from that of Experiment IV. This location was selected for the following reasons: (1) the bottom was a sandy shoal, essentially like that of the area where stream drift animals settled in the lake; (2) the water was about the same depth as that in the zone of concentration around the lakeward edge of the delta; (3) the temperature was typical of the shallow lake water on a shoal; and (4) the exposure to wave action, from which this transplant was to be protected, was similar to that near the mouth of the creek.

Experiments III and IV can be considered as controls for this experiment as they were instances in which the transplant was not protected.

Physico-chemical analyses of Carp Creek and Burt Lake waters during Experiment V revealed a close similarity of these waters, except in temperature. Data from these analyses are shown in Table 8.

TABLE 8. Data from physico-chemical analyses of Carp Creek and Burt Lake waters, July 14, 1941.

	Carp Creek	Burt Lake
Temperature (° C.).....	10.0	21.5
O <sub>2</sub> (cc./l.) .....	6.78	6.1
CO <sub>2</sub> (p.p.m.).....	0.0	0.0
Bicarbonates (p.p.m.).....	155.0	127.0
Carbonates (p.p.m.).....	10.0	14.0
pH.....	7.9	8.4
Conductivity (mho.).....	290.0	275.0

In order to isolate the small area chosen for Experiment V a bottomless bucket was thrust into the lake bottom, so as to disturb the enclosed material as little as possible, until only the upper 10 centimeters of the bucket remained above lake bottom. Transplant material was collected from the creek bottom, screened, concentrated in a cloth net, and carried immediately to the selected area. This material was placed on the sand enclosed in the partially submerged bucket. In order to avoid undue crowding only about 1 liter of concentrate was used. A loosely woven cloth was then tied securely over the top of the bucket to retain the animals within, and

yet allow free intermixture of the enclosed water with that of the lake. Thus about 1 liter of debris and creek animals was confined in a space which was 10 centimeters deep with an area equal to that of the top of an ordinary 10-quart bucket. The creek animals here were essentially like those present in the zone of concentration near the lakeward edge of the creek delta, the environment of the former differing from that of the latter in the temperature of the surrounding water and in the absence of wave action and creek current. The presence of organic debris probably reduced the dissolved oxygen content of the water in the bucket, and the concentration of animals was greater than that in the region lakeward from the creek delta; therefore the experimental conditions were less favorable for these animals than conditions existing for the drift animals, except for the protection just mentioned.

The transplant was left for one week. In order to recover the animals for study the sand was dug away from and a board was thrust under the bucket. The board served as a bottom while the bucket, the enclosed sand, and the transplant were being lifted into a tub. When the cloth was removed from the top of the bucket, most of the animals were found to be in excellent condition. Only a portion of them was saved and counted to compare number of dead animals with number of living (Table 7). Most of the animals were alive and vigorous. Several individuals of *Gammarus limnaeus* were dead, but those still alive seemed to be in good condition. It is of special interest that 314 individuals of *Tanytarsus confusus* (?) were alive, while only 17 dead individuals were found. No other dead chironomid larvae were found in the portion of the transplant examined.

Experiment VI. The data from Experiment V show that there was nothing deleterious about the lake environment, even in crowded conditions. However, as the duration of the experiment was only 1 week a similar experiment was set up and allowed to continue for 2 weeks. Location of Experiment VI was about a meter away from that of Experiment V. Methods of obtaining animals and transplanting them were those described for Experiment V. At the end of the 2 weeks most of the creek animals were active and showed no ill effects from the lake environment; Table 7 shows the number of dead animals and living ones found in the portion of the transplant examined at the end of Experiment VI. Other experiments keeping the creek animals in the lake for longer periods were not attempted, but there was no evidence to indicate that these animals might not thrive for extended periods. Experiments V and VI show that creek animals can live on lake bottom for a considerable time if protected from wave action, creek current, and predation. Environments in these experiments were less favorable than conditions existing in Experiment III and those present for drift animals located around the lakeward edge of Carp Creek delta. Since mild wave action depleted the supply of creek animals in Experiment III, and



since the drift animals in the zone of concentration around the lakeward margin of the delta at the mouth of Carp Creek were periodically washed away by waves during southerly winds, the protection from mechanical action of waves appeared to be essential for the maintenance of creek animals on the lake bottom.

#### OBSERVATIONS ON BEACH

The purpose of observations on the beach was to determine whether Carp Creek animals were washed up on the shore of Burt Lake. Most of these observations were made possible only by crawling along the shore on hands and knees. It was found that many animals on the ground were not visible from an erect position. Creek animals were detected by the following methods: (1) rapid survey of the sand and debris, confining attention to the larger and more conspicuous animals exposed on the surface; (2) careful and orderly scrutiny of every square centimeter of restricted areas; (3) a combination of studying the surface and scratching in the debris on the beach to reveal hidden animals; (4) picking debris up in the hands and carefully going over it under close observation; (5) digging down into the beach-sand and debris to reveal animals buried during recent storms; and (6) picking up a sample of beach material and sorting the animals in water in a white enamel pan. Of these methods the first was the quickest way to obtain an idea of the general distribution of animals. The last method revealed small as well as large animals present in highly variable numbers of individuals.

On August 14, 1941, after a storm from the south, the beach showed effects of severe wave action. In order to determine whether animals had been buried under the sand and debris washed upon the beach by waves, the fifth method for observation was used. Beach material was examined from various depths below the surface. Many creek animals were present as far as 4 centimeters below the surface of the sand. One living chironomid larva was found in a mass of debris covered by 10 centimeters of beach material. At that depth the debris and sand were quite wet, and the animal was able to remain alive until at least a few hours after the storm. Though water, food, and possible dissolved oxygen may have been present in the beach material in sufficient quantities to sustain lives of animals for some time, it is highly improbable that chironomid larvae could effect metamorphosis and escape from the beach. The animals in the upper few centimeters of sand almost certainly succumbed to desiccation.

Animals observed on the beach were in various conditions from moderate activity to a state of fragmentary decay. Creek animals collected on the beach were the following: *Asellus communis*, *Gammarus limnaeus*, *Nemoura venosa*, *Brachycentrus americanus*, *Prodiamesa* sp., *Trichocladius* n. sp., *Chironomus* (*Harnischia* ?) sp., and *Tanytarsus confusus* (?).

Representatives of Orthocladinae and *Endochironomus* (?) sp. also were found on the beach, but they could have been from either the creek or the lake. Individuals of *Gammarus limnaeus* and the larger larvae of Chironomidae were the most easily visible, gammarids being seen more often than any of the other animals. Almost without exception, on days when there was an abundance of animals on the beach, one or more shore birds and sparrows were seen feeding there. Tracks of birds were usually abundant on the beach.

On some days the beach east of Carp Creek was strewn with stream animals, particularly if the wind was from the southwest. When wind was from the south or southeast the animals washed up on this beach were often entirely lake species. The beach west of the creek usually had some stream animals on it if there was any considerable wave action. The more regular occurrence of creek animals on the west beach than on the east beach was probably due to the fact that the main flow of creek water in the lake was in a southwesterly direction; thus more animals drifted to the area lakeward from the west beach than to that lakeward from the east beach. The direction and intensity of the wind determined the locality where the creek animals were washed upon the beach.

On August 7, 1941, the beach west of the creek showed a series of distinct rows of debris. The row nearest the lake was the newest and had numerous living and dead animals in it, but animals in other rows had been eaten, were covered, or were in a state of odorous decay. Creek animals did not remain long on the beach. As a general rule stream animals were present along the newest row immediately after wave action.

Facts concerning animals on the beach can most easily be shown by maps. On July 21, 1941, a sand bar was present lakeward from the beach west of Carp Creek (Fig. 9). Waves broke on this bar and frequently barely washed over it. The lakeward side was free from debris. As waves washed over the bar they lost force and dropped their load of debris and animals on the sand bar's gentle shoreward slope. By the next day wave action of a storm had built up a connection between the sand bar and the beach, producing a peninsula. The debris on this peninsula contained numerous creek animals.

As waves broke over the sand bar and later over the peninsula, much of the debris and many of the animals were washed into the calm water behind the peninsula. At first this water was freely connected with the lake so that some of the animals may have made their way back to the lake. Later, because of the presence of a log on the bottom, the western end of the bay was cut off, forming a pool (Fig. 12). Wave action continued to wash animals and debris into the pool until the entire bottom was covered and a mass of debris was piled up above water level along the lakeward margin of the pool. This severely crowded pool soon became quite stagnant and odorif-

erous. It is doubtful if any of the creek animals in the pool survived.

The beach east and west of the creek was covered here and there with fallen trees, masses of roots, and piles of miscellaneous materials. Animals and debris were often entrapped in the depressions between roots, whether in the water or on shore. Most of the creek animals on the beach were less than 50 meters from the mouth of the stream. The beach was studied at varying distances from the creek in order to determine how far stream animals were carried before being washed ashore. Examination of the beach, special attention being given to collections of debris, extended from about 400 meters west to an equal distance east of the creek. No creek animals were found on the beach farther than 150 meters from the mouth of the stream.

Data obtained by observing the shore of Burt Lake proved that Carp Creek animals were washed onto the beach near the mouth of the stream during wave action. Animals on the beach were especially abundant in piles of debris. After being washed ashore, creek animals were: (1) stranded on the sand or in piles of debris; (2) eaten by birds; (3) covered by additional debris; (4) buried under layers of beach material as much as 10 centimeters thick; (5) killed by desiccation; (6) or washed into an over-crowded beach pool where death soon occurred. The direction and intensity of the wind determined where the stream animals were washed ashore.

#### RELATION OF FISHES TO DRIFT ANIMALS

It seemed pertinent to determine (1) whether fishes which frequent the area around the mouth of the stream eat creek animals, and (2) whether fishes are sufficiently abundant in that region to account for any considerable disappearance of drift animals.

During some of the experiments with transplanted creek animals minnows gathered about the areas where debris was placed on the lake bottom. Small fishes were frequently observed in the warm lake water east and west of the creek, but the only species seen in the cold water near the mouth was *Catostomus commersonnii* (Lacépède). Individuals of this species occasionally swam up into the stream. Small minnows occurred near shore about 25 meters west of the creek, and apparently fed in a mass of debris washed from the concentration zone. On one occasion a school of small fishes was seen lakeward from the mouth of the creek swimming near the surface, apparently avoiding the cold creek water below.

During the summers of 1941 and 1942, the area near the mouth of Carp Creek was seined 18 times. A minnow seine was used. Samples were collected during day and night to determine at which time fishes were more abundant in that area, and to obtain specimens for stomach examination, in order to discover whether they had eaten creek animals. Fishes

were most easily obtained shortly after midnight. On several occasions no fishes were caught.

From field observations during the entire investigation and from data (unpublished) concerning areas seined, dates, time of day or night, number and size of fish collected, and the animals contained in alimentary canals of the fishes the writer draws the following conclusions: (1) fishes were not abundant in the cold water at the mouth of Carp Creek; (2) fishes present at the mouth of the stream, and in the current of creek water in the lake, ate creek animals; (3) some fish, *Catostomus commersonnii*, *Boleosoma nigrum* (Rafinesque), and perhaps others, present in the warm lake water, fed on creek animals; (4) *Catostomus commersonnii*, especially large individuals, ate large numbers of chironomid larvae and other animals belonging to species typical of Carp Creek; and (5) fishes in this area were too few and for the most part too small to account for the disappearance of any considerable portion of the drift animals which enter Burt Lake from Carp Creek.

#### DISCUSSION

Although drifting may not be a normal event in the life of the individual animal, the occurrence of aquatic animals in the drift in the three streams studied is natural, even though the streams are not subject to flooding. The number of organisms per sample was subject to great fluctuation. Drift samples contained representatives of a wide variety of species. In general the same groups of animals were represented in all three streams, but there was considerable stream individuality so far as species were concerned.

The presence of aquatic animals in all the drift samples collected in the three streams gives evidence that the streams were constantly reducing their animal population by washing individuals away in the drift. Aquatic animals in drift samples taken at the mouth of Carp Creek, and in that part of the creek current extending out into the lake, showed that these organisms were being washed into the lake continuously. The reduction of bottom population in this stream was quite marked near the mouth of the creek.

Needham (1929) and Moffett (1936) found that erosion due to floods conspicuously reduced the population of streams. But Carp Creek is not subject to floods, consequently comparatively little erosion is present. However, the bottom is composed almost entirely of very fine sand, which shifts readily when subjected to even slight erosion. During summer, the fall of water level in Burt Lake increases the slope gradient between stream and lake. The rate of flow of creek water is increased and erosion of the bottom takes place. Erosion in 1940 and 1941 removed considerable sand from the middle of the stream bed. Most of the animals were removed from that portion of the bottom where the erosion channel

developed. Animals continued to be abundant in areas protected from erosion. The effectiveness of this erosion was probably due to the nature of the stream bottom. The abrupt entry of Carp Creek water into Burt Lake prevented the animals from settling to the stream bottom and allowed them to be washed out into the lake.

Creek water flowed well out into the lake with considerable force. The presence of creek water on lake bottom produced an environment which, during calm weather, appeared to be much like that in the stream. However, distribution of the stream animals which drifted into the lake was restricted to the area immediately lakeward from the margin of the delta. This distribution indicates either that the animals settled to the bottom very rapidly when the force of the current was somewhat reduced, or that the drift animals were being swept along the bottom of the stream and were unable to stop until they were washed over the edge of the delta.

The immediate fate of most drift animals during calm weather was to settle in the zone of concentration around the delta. Most of them were able to burrow into the lake bottom. Experiments showed that stream animals could survive the thermal and chemical conditions of the lake for at least 2 weeks. During periods of calm the population in the zone of concentration increased rapidly. However, the number of animals per bottom sample in the zone of concentration never equaled that in the uneroded areas of the stream bottom. During periods of wave action the animals were not able to burrow. Usually they were washed around the edge of the delta to a concentration of animals and debris near the beach and from there were washed up on the beach.

Periods of wave action, after irregular intervals of calm, washed most of the drift animals from the lake bottom to the beach. Death of these organisms almost certainly followed. Some of them were eaten by birds, and perhaps mammals; some were buried in beach material; and others succumbed to desiccation.

The passage of stream animals from Carp Creek into Burt Lake is influenced by, but not entirely dependent upon, the lowering of the surface level of the lake. In this situation drift animals are a loss to the stream. Most drift animals in Burt Lake probably do not complete their life cycles, but meet an early death. The death of drift animals which enter Burt Lake from Carp Creek is largely due to the action of waves in washing them upon the beach.

### SUMMARY

1. Special methods for sampling stream drift and stream and lake bottom are described.
2. A total of 71 kinds of macroscopic aquatic animals, distributed in seven phyla, have been recorded from drift in 3 streams.
3. Presence of animals in stream drift, although highly variable in quantity and quality, was the con-

stant situation. Large quantities of drift material, including animals, are carried into Burt Lake by Carp Creek.

4. In general the same larger groups of animals were represented in all 3 streams, but there was considerable stream individuality as to species. With insignificant exceptions, all species which occurred in the bottom samples from Carp Creek were sooner or later found in the drift of that stream.

5. Most of the drift animals which entered Burt Lake settled to the bottom immediately lakeward from the margin of the delta, where a zone of concentration was established. Distribution of drift animals on the lake bottom beyond the zone of concentration was not dependent upon the distribution of creek water in the lake.

6. Fall of surface level of Burt Lake affected the drift animals in the following ways: (a) increased speed of the creek current and of bottom erosion for at least 85 meters upstream from the mouth; (b) altered quantity and probably quality of drift animals entering the lake; (c) caused lakeward extension of the delta; and (d) exposed drift animals, in concentration zone, to more vigorous wave action.

7. Observations and experiments showed that drift animals could maintain positions on the lake bottom during the absence of, or while protected from, wave action.

8. Wave action affected the drift animals in the following ways: (a) prevented burrowing; (b) partially or completely depopulated the zone of concentration; (c) washed animals upon the beach near the creek; and (d) changed the position of delta materials to form islands, spits, and sand bars upon which creek animals were stranded.

9. Creek animals on the beach met the following fates: (a) were buried in beach material; and (b) succumbed to desiccation. Predatory activities of fishes accounted for disappearance of only a minor portion of the drift animals which entered the lake.

10. Most of the animals drifting from Carp Creek into Burt Lake did not survive for extended periods of time. The major factor in the lake environment which determined the fate of drift animals was wave action.

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